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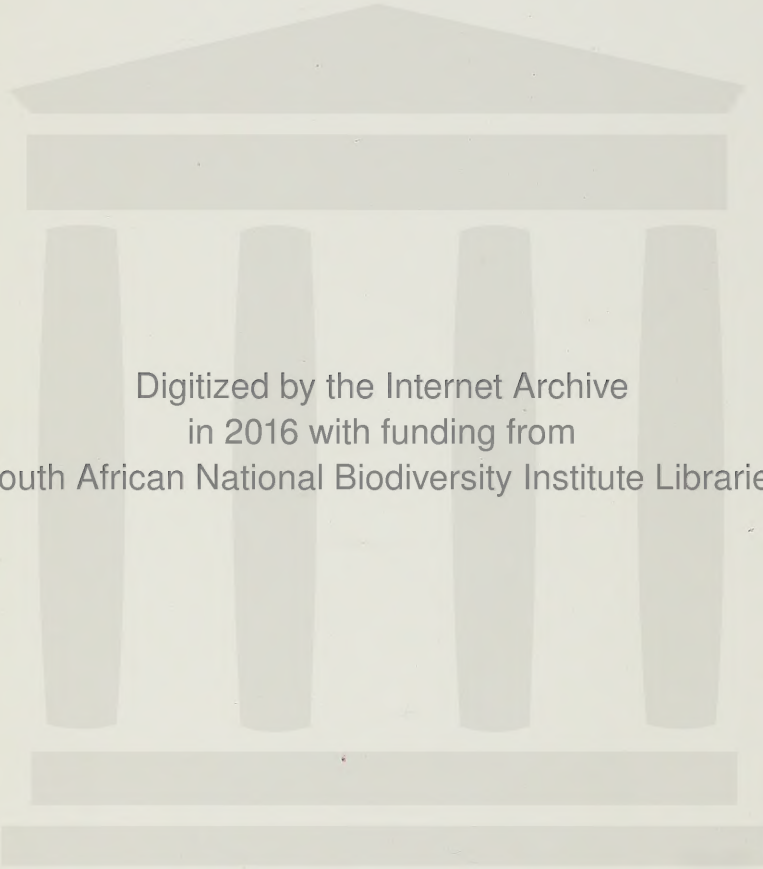
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JOURNAL OF SOUTH AFRICAN BOTANY

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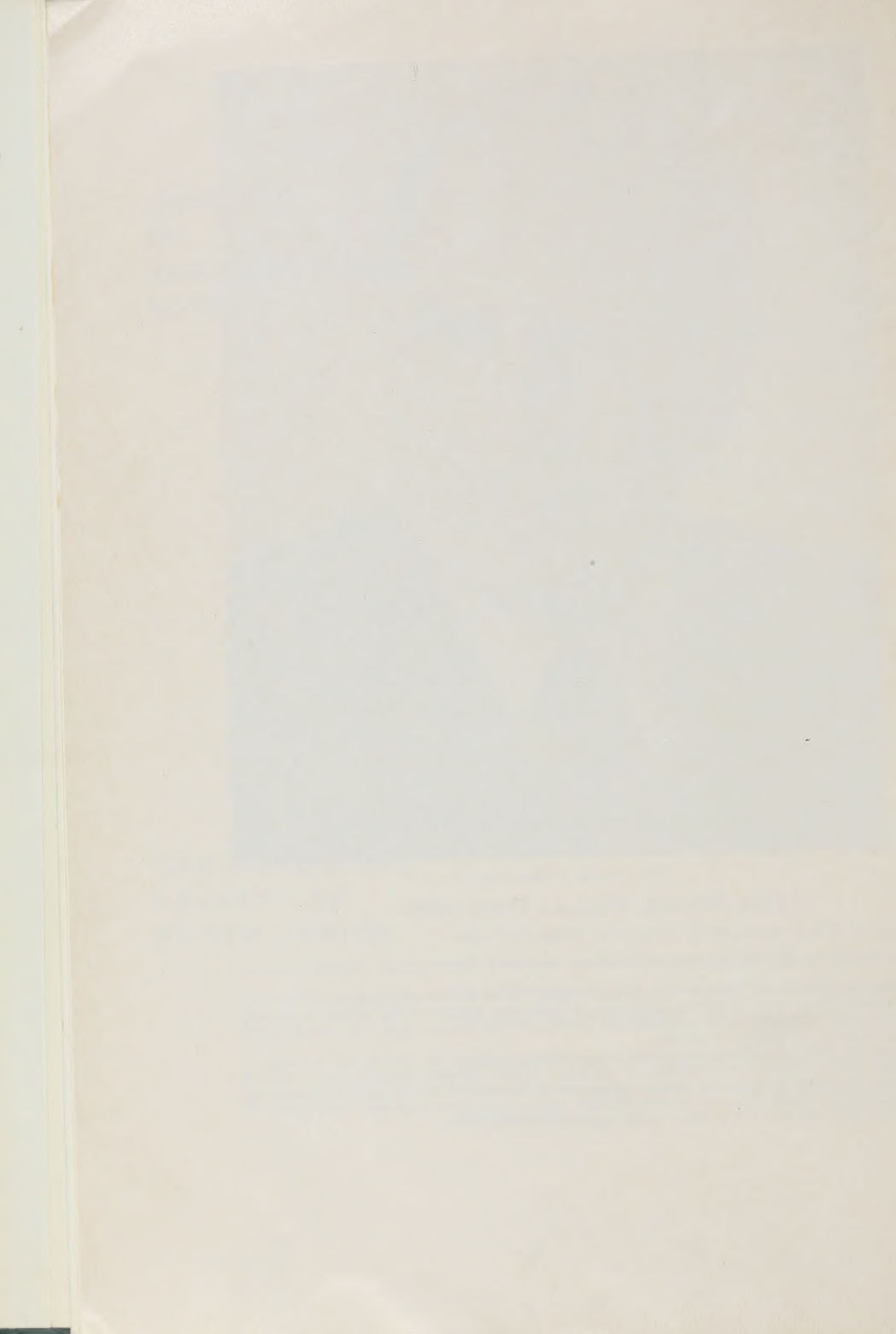
LESLIE EDWARD WOSTALL CODD (1908—)

D.Sc.

(*Director of the Botanical Research Institute, Department of Agricultural Technical Services.*)

Editor of Flowering Plants of Africa and Bothalia; editor of Flora of Southern Africa. Well-known for his book "The Trees and shrubs of the Kruger National Park" and for his revision of the South African species of *Kniphofia*, *Schotia*, *Albizia*, *Cloeme* (with L. E. Kers), Apocynaceae and researches in Labiatae.

He has held executive positions in several scientific societies: in 1958 he was president of Section B of S2A3; 1961 president of the South African Biological Society and in 1968 the first president of the South African Association of Botanists. One of his special interests has been the Pretoria National Botanic Garden, which he has seen developed from practically bare veld to one of the premier botanic gardens in South Africa.



EUPHORBIA SPECIES FROM THE FLORA ZAMBESIACA AREA: 10

L. C. LEACH

ABSTRACT

In this, the tenth in the series, three new species of *Euphorbia* are described; *E. mlanjeana*, from Malawi; *E. fanshawei*, from northern Zambia and *E. decliviticola* from northern Mozambique, and their apparent relationships discussed. *Euphorbia johnsonii* is reduced to subspecific rank in *E. knuthii*, which has a distribution in Mozambique, Transvaal and Natal.

UITTREKSEL

EUPHORBIA SOORTE VAN DIE FLORA ZAMBESIACA AREA: X

In hierdie, die tiende van die reeks, word drie nuwe *Euphorbia* soorte beskryf; *E. mlanjeana* vanaf Malawi; *E. fanshawei* vanaf Noord-Zambia en *E. decliviticola* vanaf Noord-Mosambiek en hulle skynbare verwantskap word bespreek. *Euphorbia johnsonii* word verlaag tot 'n subspesie van *E. knuthii* wat in Mosambiek, Transvaal en Natal voorkom.

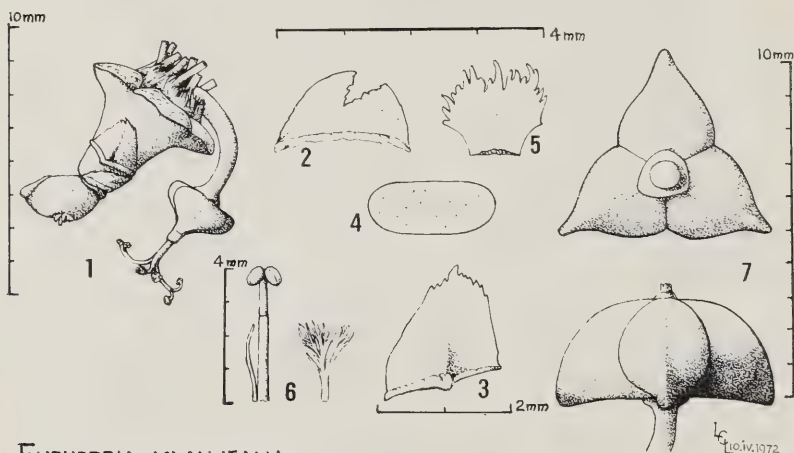
Previous articles in this series have appeared in Jl S. Afr. Bot. **30**: 1-12, 209-217 (1964); **31**: 241-249 (1965); **32**: 173-182 (1966); **33**: 247-262 (1967); **35**: 13-23 (1969); **36**: 13-52 (1970); and in Kirkia **4**: 15-23 (1964); **6**: 133-145 (1968).

Euphorbia mlanjeana Leach, sp. nov.; *E. graniticolae* Leach affinis sed planta parviore; ramis gracilioribus brevioribus, segmentis plerumque longioribus 3-6 alatis, alis tenuioribus podariis spinisque debilibus, podariis plerumque separatis; foliis parvissimis; inflorescentia unicymosa, cyma horizontaliter disposita distinctissima.

Frutex arboreus, succulentus, spinosus, acaulescens vel trunco brevi, crasso, cylindrico, nudo, griseo vel saepe ignibus denigrato, ramis confertis, fere rectis vel leviter curvatis patenti-ascendentibus apice coronato, usque ad 1 m altus (plerumque brevior), in locis praecipitibus crescens. *Rami* usque ad 0.6 m longi, plerumque breviores, c. 3 cm diam., interdum in segmenta proportionem longa leviter constricti, 3-5(6)-alati; alis usque ad 1,2 cm latis, 1,5-2 mm crassis, margine sinuato podariis spinisque infirme armato; *podaria* decurrentia initio separata demum plerumque fere vel satis confluentia; *spinae* binae valde divaricatae, horizontaliter patulae, 4-4,5 mm longae, 6-12 mm (plerumque plus minusve regulariter 10 mm) secus angulos distantes. *Folia* sessilia linearia vel anguste-ovata, acuta, 3-4 mm longa, plus minusve 1 mm lata, mox decidua; cicatrice plus minusve circulari, spinulis binis rudimentalibus late dispositis. *Inflorescentia* glabra, flava, unicymosa, plus minusve 2 mm supra spinas inserta; cyma pedunculata, pedunculo brevissimo, bibracteato; bractae parvissimae squamiformes; cyathii 3 horizontaliter dispositi; cyathium medium masculinum mox deciduum; cyathia lateraliter bisexualia in cymarum ramis brevibus

Accepted for publication 25th May, 1972.

portata. *Involucrum* plus minusve obconicum, c. 2,5 mm longum, 4-4,5 mm diam.; *glandulis* 5, carnosius, valde patulis, contiguis, transverse oblongis, 1,5-2 mm $\times$ 0,75 mm, flavis, superficie leviter foveolato-rugulosa; *lobis* 5, plus minusve obovatis c. 1,6 mm latis, 1,4 mm longis, irregulariter fimbriatis paulo bilobatis vel emarginatis. *Flores masculini* c. 15, 5-fasciculati, bracteolis filiformibus vel filiformi-fimbriatis; *pedicelli* 2,5-3 mm longi; *filamenta* c. 1,25 mm longa. *Ovarium* plus minusve triangulare basi truncatum, ex involucrio pedicello curvato exsertum; *ovulum* obturamento cuculliformi, paulo bilobato, minute dentato suspensum. *Styli* c. 2,25 mm longi graciles, in columnam c. 1,25 mm connati, partibus libris valde patulis fere rectis, apicibus breviter bilobatis capitatis, granuloso-rugulosis. *Capsula* 3-lobata, plus minusve triangularis basi truncata apice parum rotundata, 6-7 mm inter angulos, c. 3 mm alta, longe ex involucrio exserta; *pedicello* initio valde recurvato demum erecto, usque ad 8 mm longo, basi c. 1 mm diam. apicem versus gradatim decrecenti ad c. 0,5 mm diam.; *perianthio* rudimentali, obtuse triangulari, c. 1 mm diam. *Semen* subglobosum, c. 2 $\times$ 2,25 mm, laeve, brunneum; sutura angusta leviter prominenti.



EUPHORBIA MLANJEANA

FIG. 1.

- (1) Cyathium (2) Bract subtending cyme branch (3) Involucral bract (4) Involucral gland
(5) Involucral lobe (6) Male flower, bracteole and fascicular bract (7) Capsule

Typus: MALAWI, Mlanje Mountain, *Leach et al* 14805 (K; LISC; PRE; SRGH, holo.).

Malawi. S: Mlanje Mountain, steep exposed slopes above Little Malosa Riv., near the entrance to "The Crater", st. 15.viii.1971, *Leach et al* 14805 (K;

LISC; PRE; SRGH); idem, cuttings cult. Salisbury, fl. 30.x.1971, *Leach* 14805A (K; LISC; PRE; SRGH); ibid. fr. Jan. 1972, *J. & M. Royle* in *Leach* 14805B (BR; K; LISC; PRE; SRGH); slopes above Ruu gorge, Lujeri Tea Estate, st. 17.viii.1971, *Leach et al* 14823 (BR; FHO; K; MAL; SRGH), ibid. seedlings, 14823A (K; SRGH).



FIG. 2.

Plant at type locality above Little Malosa River lower slopes of Mlanje Mountain.
Euphorbia mlanjeana *Leach et al* 14805

E. mlanjeana appears to be restricted to exposed precipitous granite slopes above river gorges on the lower slopes of Mlanje Mountain, among grasses and vellozia. It appears to be most closely related to *E. graniticola* among the species presently known, although differing therefrom in several important respects.

The shorter, more slender, relatively long-segmented, 3–6-winged branches of the new species, which appear to persist at most for only a few seasons, are very different from those of its relative; while the thin wings armed with weak spines arising from small, usually separate spine shields contrast quite sharply with the more strongly armed and continuously margined, stout branches of the more southerly species, which are known (from plants in cultivation) to

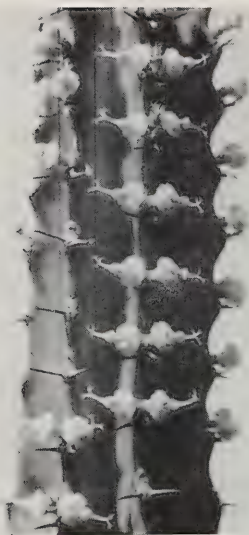


FIG. 3.
Cutting at early flowering stage

Euphorbia mlanjeana

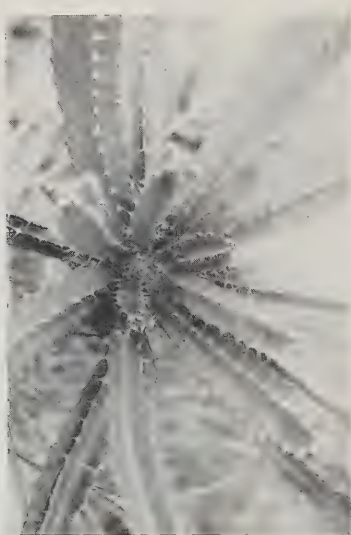


FIG. 4.
Apex of trunk, showing central
development of branches
Leach et al 14805

persist for at least 15 seasons. However, it is probably in the arrangement of the inflorescence that the most significant divergence occurs: that of *E. graniticola* comprises 1–3 cymes, each of three vertically arranged cyathia, as opposed to the more simple arrangement of a single cyme of three horizontally arranged cyathia which is characteristic of the new species.

There are other less important differences between the two taxa, e.g. the generally smaller stature of the Malawian plants and their much shorter leaves. However, a similarity in their manner of growth seems to be worthy of mention; on first sight Mr. Whellan described this as being similar to that of *E. decidua* Bally & Leach (a tuberous-rooted species with annual spiny branches arising from a single crown), and the simile is by no means inappropriate, especially when the trunks of *E. mlanjeana* have been almost stripped of their branches by grass fires (which appear to be frequent). New branches arise from the centre of the crown in exactly the same fashion as is normally met in some of the tuberous-rooted species; and the same arrangement, although less marked, is to be seen in *E. graniticola* but not in the related *E. decliviticola* Leach (described elsewhere in this paper). This is one of several reasons why *E. mlanjeana* is considered to be more closely related to the former, despite the latter's geo-

graphical proximity; another being the more nearly similar capsule shape of the more southerly species.



FIG. 5.

Unusual branched plant, Ruu Gorge, above Lujeri Tea Estate. *Leach et al* 14823
Euphorbia mlanjeana

On the rock slopes inhabited by *E. mlanjeana* the development of a below-ground stem would be impossible; it will be interesting, therefore, to see if seedling plants now in cultivation on deeper soils will maintain the trunk-forming habit or whether they will develop an underground stem, which would somehow seem to be more in conformity with their manner of growth.

In his "The Vegetation of Mlanje Mountains" (1962), J. D. Chapman mentions a small, candelabra-type euphorbia which is represented by his gathering No. 312. This specimen differs in several respects from the species now described; e.g. the inflorescence is of the pattern with three vertically-arranged cymes. This is, unfortunately, insufficiently developed for identification.

It seems, therefore, that there are two euphorbias, of somewhat similar appearance, growing on Mlanje Mountain and it is hoped to make the second of these the subject of further investigation as it does not appear to belong in any of the currently known species from this part of Africa.

Plant: a succulent, spiny, often tree-like, small shrub, up to ± 1 m high (usually shorter), acaulous or with a short (seldom attaining 0,5 m in height), stout (± 10 cm diam.), cylindric, nude trunk, grey or frequently blackened by grass fires; with a crown of crowded, almost straight or slightly curved, spreading, ascending branches. *Branches* up to 0,6 m long (generally less), ± 3 cm diam., narrowing towards the base, sometimes slightly constricted into 2–3 relatively long segments; 3–5(6)-winged, with thin wings up to 1,2 cm wide, 1,5–2 mm thick at the weakly-armed sinuate toothed margin and scarcely thicker at their junction with the small central core. *Spines* in pairs, widely divergent ($\pm 120^\circ$ – 170°), horizontally spreading, of remarkably uniform length (when fully developed), 4–4,5 mm long, 6–12 mm, mostly more or less regularly ± 10 mm apart along the angles; *spine shields* initially separate, decurrent to an acute point below and similarly produced above to include the flowering eye ± 2 mm above the spine pairs, usually becoming confluent into a continuous or sub-continuous horny grey margin with age. *Leaves* sessile, linear or narrowly ovate, acute, 3–4 mm long, ± 1 mm wide, caducous, leaving a $\pm$ circular scar flanked by a pair of widely-spaced, often obsolescent, rudimentary prickles. *Inflorescence* glabrous, yellow, comprising a single, very shortly pedunculate cyme of three horizontally arranged cyathia; *peduncle* bibracteate, with very small, scale-like bracts subtending the short cyme branches; the initial, central cyathium male, deciduous, and the lateral cyathia bisexual. *Involucre* more or less obconic, $\pm 2,5$ mm long, 4–4,5 mm diam.; *glands* 5, fleshy, widely spreading, contiguous, transversely oblong 1,5–2 mm $\times$ 0,75 mm, yellow, with the upper surface pitted rugulose; *lobes* 5, more or less obovate, $\pm 1,6$ mm wide $\times$ 1,4 mm long, irregularly fimbriate, slightly 2-lobed or emarginate. *Male flowers* $\pm 1,5$, arranged in five fascicles with filiform or filiform-fimbriate bracteoles; *pedicels* 2,5–3 mm long; *filaments* $\pm 1,25$ mm long. *Ovary* more or less triangular, truncate at the base, exserted from the involucre on a curved pedicel; ovule suspended under a minute, hood-shaped, somewhat 2-lobed, minutely denticulate obturator. *Styles* $\pm 2,25$ mm long, slender, united into a column $\pm 1,25$ mm long, with the free portions widely spreading, almost straight, with the capitate apices shortly 2-lobed and granulate rugose stigmas. *Capsule* 3-lobed, more or less triangular with the base sharply truncate and the apex somewhat rounded, 6–7 mm across the angles, ± 3 mm high, far exserted from the involucre; *pedicel* initially strongly recurved, becoming straight and erect shortly before dehiscence, up to 8 mm long, ± 1 mm diam. at the base tapering gradually to the $\pm 0,5$ mm diam. apex; *perianth* rudimentary, obtusely triangular, ± 1 mm diam. *Seed* subglobose, $\pm 2 \times 2,25$ mm, smooth, brown with a narrow slightly-raised suture.

***Euphorbia fanshawei* Leach, sp. nov.**

E. decidua Bally & Leach arcte affinis sed ramis prominentissime tuberculato-

dentatis; inflorescentia brevissime pedunculata, semper in ramis portata nunquam caudice exorienti; bracteis parvissimis; involucri proportionem brevioris lobis latioribus brevius fimbriatis; perianthio valde dentato-trilobato bene distincta.

Herba pumila perennis; ramis succulentis, spinosis. *Radix* tuberosa, nappiformis vel sphaeroidea. *Caulis* redactus, hypogaeus radici coalescens. *Rami* caudicis ab apice radiantes, plerumque numerosi, simplices, aliquantum clavati, initio patenti-erecti, demum flaccidi saepe decumbentes, usque ad 12,5 cm longi, (4)5–6-angulati, prominentissime tuberculato-dentati; *dentibus* carnosus usque ad 7 mm altis (basin versus decrescentibus), secus angulos instructi. *Dentes* scutulo badio, superficiali, plus minusve sub-quadrato, bispinoso muniti; *spinis* binis, divergentibus, basibus inflatis e scutulo procurrentibus, late patentibus rarissime deflexis, usque ad 4 mm longis (plerumque brevioribus). *Folia* carnosae, erecta, subconchoidea, acuta, ad 2,5 mm longa, super scutulum prodientes; aculeo in quoque latere instructa. *Inflorescentia* axillaris, saepe cyathio bisexuali solitario, breviter pedunculato, interdum cymosa pedunculo usque ad 5 mm longo; cyathio initio masculo marcescenti cyathiisque lateralibus bisexualibus in ramis usque ad 4 mm longis portatis, raro cyathiis lateralibus secundariis prodientibus; cymae ramis bractea squamiformi parvissima subtentis. *Cyathium* glabrum plus minusve late turbinatum, c. 2–2,5 mm longum, usque ad 5 mm diam.; *glandulis* 5, carnosae, patulis, transverse oblongis, contiguas, leviter convexae, flavae, foveolatis, c. 2–2,25 mm × 1 mm; *lobis* 5, imbricatis, plus minusve transverse late ellipticis irregulariter fimbriatodentatis, basin versus leviter carnosae, c. 1 mm longae, ad 2 mm latae; *bracteis* squamiformibus, ad apicem minute denticulatis, c. 1 mm longe lateque. *Flores masculae* c. 20, bracteolis filiformibus 5-fasciculatis; fasciculis unusquisque bractea subtiliter filiformis vel plumoso-lobata instructis; *pedicelli* c. 2,5 mm longi; filamenta c. 1 mm longa. *Ovarium* pedicello recurvato longe exsertum; *ovulum* laeve ecarunculatum, obturamento minute denticulato suspensum; *styli* 3–3,5 mm longi in columnam breviter connati, patuli, apicibus rugulosis, capitatis aut emarginatis aut breviter bilobatis. *Capsula* fere maturescens, 3-lobata, angulis subacutis, in sinibus manifeste costata, c. 3 mm diam., 2,25 mm alta; *perianthio* profunde dentato-trilobato, c. 2,25 mm inter apices loborum. *Semen* maturum non visum.

Typus: ZAMBIA, Kawambwa Distr., Williamson & Drummond 1985A (BR; K; SRGH, holo.).

Zambia. N; Northern Prov., Kawambwa Distr., immature ♂ fl., 24.viii.1957, Fanshawe F3590 (NDO); ±16 km W of Kawambwa, ±9° 52' S; 28° 55' E, in sandy soil on quartzite outcrop in *Brachystegia* woodland, near river above Ntumbachushi Falls, st. 24.xii.1967, Williamson & Simon 726 (PRE), idem cult. SRGH, fl. 10.vi.1970, 726A (SRGH); ibid. st. 27.ii.1970, Williamson & Drum-

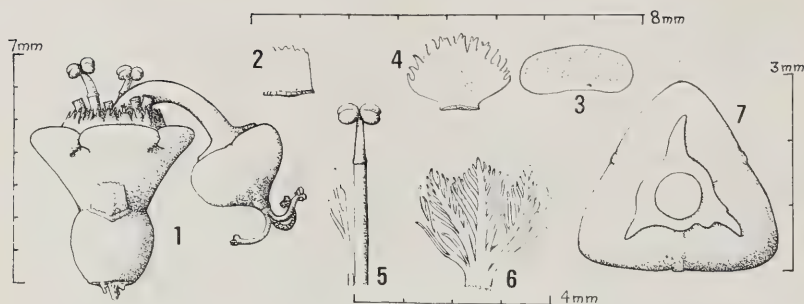


FIG. 6.

1. Cyathium 2. Involucral bract 3. Involucral gland 4. Involucral lobe
5. Male flower with bracteole 6. Fascicular bract 7. Capsule (nearly fully developed).
***Euphorhorbia fanshawei* Leach**

mond 1985 (G; SRGH), idem cult. SRGH, fl. 10.iv.1972, 1985A (BR; K; SRGH).

This interesting new species appears to be very closely related to the comparatively widespread *E. decidua* but nevertheless differs in a number of characters; the most obvious among these being its more prominently tuberculate toothed branches. The inflorescence of *E. fanshawei*, unlike that of its relative, is developed only on these branches, which appear to persist under natural conditions for more than a full season; with the inflorescence appearing quite late in the growing cycle, e.g. *Fanshawe* F3590, which is at an early stage of flowering in late August.

That the hysteranthous habit of *E. decidua* has developed in response to the drier conditions in which it grows seems evident from the fact that under presumable abnormal conditions of water availability in cultivation, this species sometimes produces an inflorescence on its branches, similar in all essentials but additional to that arising direct from the caudex. This trait, although not unknown even under natural conditions among other geophytes of the tribe, e.g. *E. trichadenia* Pax, has never been observed in plants of *E. fanshawei* in cultivation. Individuals of this latter species, when subjected to conditions of dryness approaching those under which *E. decidua* normally grows, usually die or occasionally produce an inflorescence on very young undeveloped new branches; a response in all ways similar to, yet falling far short of that developed in *E. decidua*. There are other important differences which include the shorter peduncle of the new species (the longest seen being shorter than the shortest seen in *E. decidua*) and its proportionally shorter involucre with wider, less deeply fimbriate lobes and a deeply lobed, much larger perianth; while the very much smaller bracts of the inflorescence of *E. fanshawei* appear to be infallibly



FIG. 7A.

Young plant showing leaves and spinescence *Williamson & Drummond 1985A*

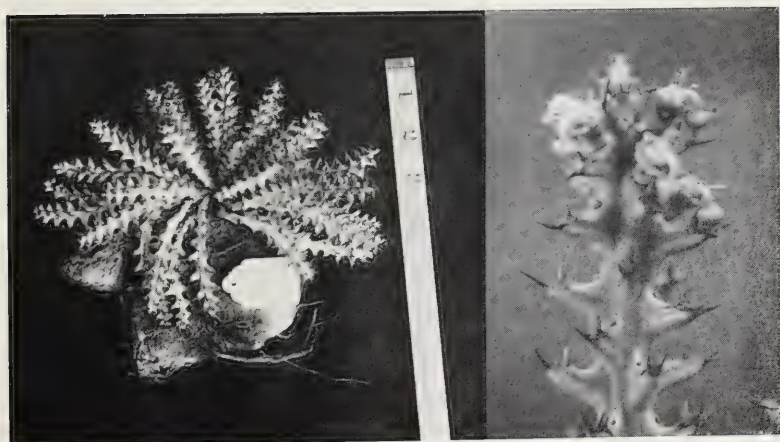


FIG. 7B.

Mature plant with flattened tuber
Williamson & Drummond 1985

Flowering branch
1985A

Euphorbia fanshawei

diagnostic. There are also several minor differences, such as the set of the paired spines which in the Kawambwa plants are usually horizontally spreading or somewhat ascending, as opposed to the generally more or less deflexed spine pairs of *E. decidua* which are also usually more widely divergent; while the anthers of the new species are, in the material seen, noticeably smaller than those of its relative.

The distribution of *E. fanshawei* as presently known appears to be restricted to a limited area in the vicinity of Ntumbachushi Falls, some 16 km to the west of Kawambwa in the Northern Province of Zambia. Here plants are fairly plentiful, growing in very humid conditions on shallow quartzitic soil in woodland shade; a habitat which it shares with *E. williamsonii* Leach, which is also, as far as is known, endemic to the same area.

Plant: a dwarf perennial herb with a turnip-shaped or more or less oblate tuberous root, with succulent spiny branches radiating from the apex of the much reduced, subterranean stem which merges imperceptibly with the root. *Branches* usually numerous, simple, somewhat clavate, initially erectly spreading, becoming flaccid and often decumbent with age, up to 12.5 cm long, (4)5–6-angled, with prominent fleshy tubercle teeth up to 7 mm high (becoming smaller towards the base) along the angles. *Spines* in widely spreading or somewhat ascending (very rarely deflexed) divergent pairs, up to 4 mm long (usually shorter), with inflated bases, extended from the outer margin of the dark or reddish brown, subquadrate *spine shield* on the upper surface at the apex of the tubercle teeth. *Leaves* fleshy, subconical, acute, erect, up to 2.5 mm long, quite or nearly touching the spine shield, which extending on each side of the leaf base but not enclosing it carries the pair of prickles, which initially touching the leaf base become somewhat distant as the spine shield develops. *Inflorescence* axillary, sometimes cymose or often comprising a shortly pedunculate, solitary, bisexual cyathium; when cymose, with a peduncle up to 5 mm long and the initial cyathium male, marcescent, with the lateral bisexual cyathia borne on cyme branches up to 4 mm long, less frequently with secondary lateral cyathia developing on each side of the first; cyme branches subtended at their base by a very small scale-like bract. *Cyathium* glabrous, more or less broadly obconical, ± 2 –2.5 mm long, 5 mm diam.; *glands* 5, fleshy, spreading, transversely oblong, ± 2 –2.5 mm $\times$ 1 mm, contiguous, yellow on their slightly convex, pitted upper surface; *lobes* 5, imbricate, more or less transversely broadly elliptic, ± 2 mm wide, 1 mm long, irregularly fimbriate toothed, slightly fleshy towards the base; *involucral bracts* scale-like, minutely toothed at the apex, ± 1 mm long and wide. *Male flowers* ± 20 , with filiform bracteoles, arranged in 5 fascicles, each with a finely filiform-divided or plumose lobed inner bract; *pedicels* ± 2.5 mm long; *filaments* ± 1 mm long. *Ovary* far exserted on a recurved fleshy pedicel; *ovule* smooth, without a caruncle, suspended under a minutely denticulately fringed

obturator; styles 3–3,5 mm long, shortly united at their base, with the free portions widely spreading, with capitate or emarginate, or sometimes shortly bilobed, rugulose apices. Capsule nearing maturity, 3-lobed with subacute angles, distinctly ribbed in the sinuses, ± 3 mm diam., 2,25 mm high; perianth dentate, deeply 3-lobed, $\pm 2,25$ mm across the apices of the lobes. Fully mature capsule and seed not seen.

***Euphorbia declivicola* Leach, sp. nov.**

E. graniticola Leach arcte affinis sed planta semper caulescenti, ramis verticillatis, florescentia aestivali; inflorescentia cymis cyathiisque temere dispositis; involucri lobis fere duplo latioribus et florum masculorum fasciculis bractea lata laciniata interne subtentis; capsula fere subglobosa differt.

Arbuscula succulenta, spinosa, usque ad 3 m alta, caulescens; *trunco* crasso, demum multi-angulato, ramorum verticillatum delapsum cicatricibus cingenti-notato; ramis persaepe simplicibus verticillatim arcte contiguis coronato. *Rami* patentes arcuato-ascendentes, 4–6-angulati, c. 0,6 m longi, in segmenta constricti, segmentis 2,5–15 cm longis, angulis alatis, alis 2–2,5 cm latis, albo-marginatis; margo corneus, continuus, 1,5–3 mm latus. *Spinae* binae divaricatae plus minusve horizontaliter patulae, usque ad c. 6 mm longae. *Folia* sessilia, carnosa, caduca, ovata vel anguste ovata, acuta, usque ad 7 mm longa; foliorum cicatricibus subcircularibus vel late obovatis mox inconspicuis spinulisque obsolescentibus. *Inflorescentia* cymosa, cymis 1–3 brevissime pedunculatis temere dispositis, unaquibusque initio cyathiis 3 temere (frequenter horizontaliter vel oblique) dispositis; cyathio medio masculo sessili deciduo, cyathiis lateralibus bisexualibus, plerumque cyathiis bisexualibus secundariis bractearum axillis exorientibus, interdum cyathiis bisexualibus itidem crebro effectis. *Pedunculus* bracteatus, c. 2 mm longus $\times$ 3 mm crassus, bracteis plus minusve lunatis plerumque scissis; cymarum ramis c. 2 mm longis, bracteis binis initio plus minusve ovatis, minute denticulatis mox laceratis. *Involucrum* glabrum, truncato-obconicum 2,5–3,25 mm longum, plerumque c. 4,5–5 mm diam.; *glandulis* 5, carnosae, separatis vel fere contiguis, plus minusve depresso obovatis, 1,75–2,5 mm latis $\times$ c. 1 mm, leviter convexis, sparse leviter rugulosae, peranguste laevi-marginatis, flavis; *lobis* 5, subquadratis vel transverse oblongis, usque ad 1,75 mm latis, profunde fimbriatis. *Flores masculi* c. 30, bracteolis filiformibus vel filiformi-laceratis, 5-fasciculati; fasciculis unusquisque bractea lata laciniata apice subtiliter filiformi-lacerata interne subtentis; *pedicelli* c. 3 mm longi; *filamenta* c. 1,5 mm longa. *Ovarium* subglobosum pedicello curvato exsertum; ovulum obturamento minimo sublobato dependens; *styli* c. 1 mm longi, libri fere ad basim, patuli, apice brevissime bilobati. *Capsula* obtuse trilobata, fere subglobosa, 5–5,5 mm diam., 3–3,5 mm alta ubi plus minusve matura; pedicello usque ad 7 mm longo, perianthio obtuse triangulari vel fere subcirculari, usque ad 2,5 mm diam. *Semen* globosum c. 2 mm diam. laeve.

Typus: MOÇAMBIQUE, Moçambique Distr., *Leach & Schelpe* 11427 (K; LISC; PRE; SRGH, holo.).

Moçambique. N: Moçambique Distr., ± 18 km E of Namina, st. 23.v.1961, *Leach & Rutherford Smith* 10976 (K; LISC; PRE; SRGH); $\pm 2,5$ km S of Posta Agricola, Ribaué, cult. Nelspruit, fl. & fr. Nov. 1969–Jan. 1970, *Leach & Schelpe* 11427 (K; LISC; PRE; SRGH).

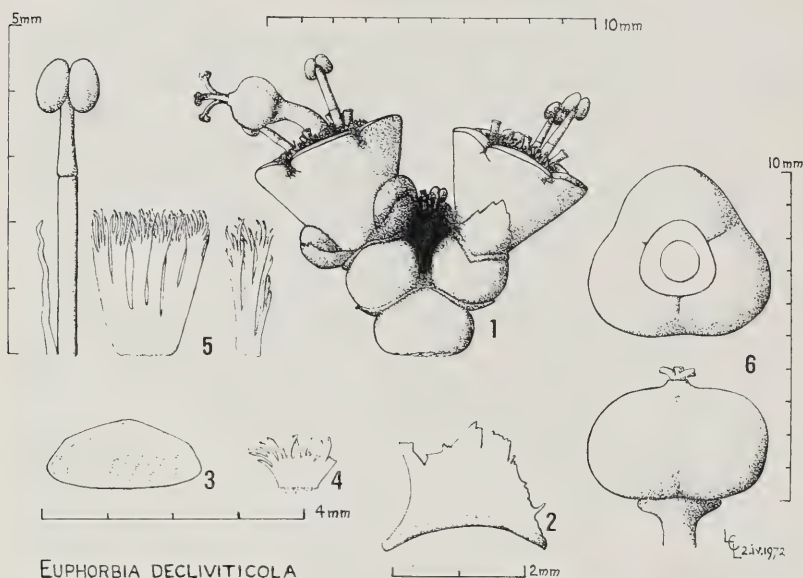


FIG. 8.

1. Cyme with lateral bisexual cyathia 2. Bract subtending cyme branch 3. Involucral gland 4. Involucral lobe 5. Male flower with bract and bracteoles 6. Capsule in elevation and plan

Euphorbia decliviticola appears to be most closely related to *E. graniticola* from the Manica District of Moçambique, some 700 km to the south-west of the distribution of the new species. Both taxa occupy similar habitats on exposed granite slopes but that now described differs from its relative in being essentially caulescent with whorled branches, whereas *E. graniticola* comprises primarily acaulescent shrubs with crowded branches arising from a much reduced multi-angled crown which develops into a cylindric trunk only very gradually. The inflorescence of *E. decliviticola*, while similar in many respects to that of *E. graniticola*, has the cymes randomly arranged with their cyathia often horizontally or obliquely arranged with secondary and tertiary bisexual cyathia fre-

quently developing. The fascicles of male flowers of the new species are subtended internally by a broad, laciniate, finely fimbriate bract and on the outside by a fimbriate toothed, transverse lobe which is almost twice as wide as that of its southerly relative. The slightly smaller, more nearly globose capsule of *E. declivicola* is borne on a somewhat shorter pedicel, and finally these northerly plants flower in midsummer as opposed to the somewhat erratic but normally winter or spring flowering of *E. graniticola*.



FIG. 9.

Euphorbia declivicola Leach

Mr. R. Rutherford-Smith with plant on granite slope, between Namina and Nampula.
Leach & Rutherford-Smith 10976

These differential flowering periods have been retained in cultivation over a number of years; this has resulted in the difficulty experienced in obtaining material adequate for the description of the new species. Heavy rain or hail has so often caused abortion of the immature cyathia, while for three consecutive seasons hail has actually smashed many of the branches of plants grown at Nelspruit in the Easter Transvaal. Somewhat similar conditions possibly obtain in its natural habitat and may account, in part at least, for the paucity of young plants and seedlings seen at either of the known localities.



FIG. 10.

Population of *E. decliviticola* between Namina and Nampula

Juveniles of *E. graniticola* are acaulescent with numerous, crowded, usually spirally twisted branches from a many-angled, much-reduced crown, while those of *E. decliviticola* are produced rather sparingly from an initially 4-angled erect stem which eventually develops into the multi-angled trunk of the species. This trunk remains somewhat angular and is plainly marked by the scars of fallen branches, whereas that of its relative, which is developed very slowly, is relatively smooth and cylindric.

The photograph of a young plant of *E. decliviticola* depicts a juvenile estimated to be 12–15 years old, while that of a shrub of *E. graniticola* is known to be considerably older as this was already a shrub when originally collected some 16 years ago.

Plant a succulent, spiny small tree or tree-like shrub, up to ± 3 m tall, with a stout, eventually multi-angled simple trunk which is clearly marked with rings of scars of the fallen branches and crowned with a head of crowded, verticillately arranged, mostly simple, winged, spiny branches. Branches spreading, arcuate ascending, $\pm 0,6$ m long, constricted into 2,5–15 cm long, mostly oblong segments, generally ± 6 cm thick with 4–6 wing-like angles; the wings 2–2,5 cm broad with a continuous, whitish, horny margin 1,5–3 mm wide. Spines in divergent pairs, more or less horizontally spreading, up to ± 6

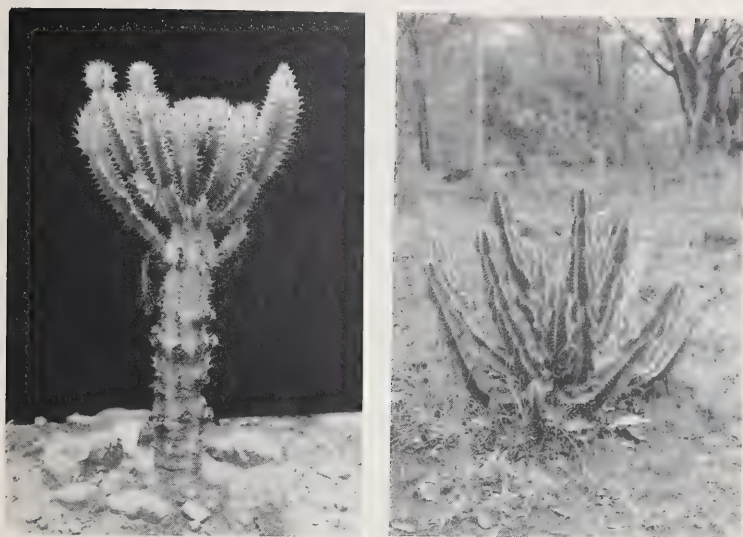


FIG. 11.

E. decliviticola
estimated age 12-15 years.

E. graniticola
age known to be well over 16 years.

A comparison of young plants.

mm long. *Leaves* fleshy, caducous, sessile, ovate or narrowly ovate, acute, up to 7 mm long, with the subcircular or broadly ovate scars soon becoming inconspicuous and the flanking prickles obsolescent. *Inflorescence* cymose, with 1-3 shortly pedunculate, randomly arranged cymes, each initially bearing 3 randomly (often horizontally or obliquely) arranged cyathia, with the sessile initial cyathium male deciduous and the laterals bisexual; these latter often with secondary bisexual cyathia arising from the axils of their bracts and sometimes with further bisexual cyathia repeatedly developing. *Peduncle* bibracteate, ± 2 mm long $\times$ 3 mm thick; *bracts* more or less lunate, but usually split and deteriorated; *cyme branches* ± 2 mm long and thick, with a pair of bracts which are initially more or less ovate with minutely denticulate margins but soon become split and torn as the cyme develops. *Involucre* glabrous, truncate obconic, 2.5-3.25 mm long, usually ± 4.5 -5 mm diam.; with 5 separate or barely contiguous, fleshy, more or less depressed obovate yellow glands, 1.75-2.5 mm $\times$ ± 1 mm, sparingly lightly rugulose on the slightly convex upper surface and with a very narrow smooth margin, and 5 subquadrate or transversely oblong, deeply fimbriate lobes up to 1.75 mm wide. *Male flowers* ± 30 , arranged in 5 fascicles with filiform or filiform lacerate bracteoles, each

fascicle subtended internally by a broad laciniate finely fimbriate bract. *Ovary* subglobose, exerted from the involucre on a curved pedicel; ovule suspended under a very small, slightly 2-lobed obturator; *styles* ± 1 mm long, free almost to the base, spreading, with very shortly bifid apices. *Capsule* obtusely 3-lobed, almost subglobose, 5–5.5 mm diam., 3–3.5 mm high when almost mature; with a pedicel up to 7 mm long and an obtusely triangular or almost subcircular perianth up to 2.5 mm diam. *Seed* globose, ± 2 mm diam., smooth.

***Euphorbia knuthii* Pax**

Subsequent to the rediscovery, in 1961, of *E. johnsonii* N.E.Br. on the Moçambique coast to the north of the Savé River, the author has had the opportunity of investigating a number of localities between Delagoa Bay and Beira, which appeared to be suitable for the occurrence of either *E. knuthii* or *E. johnsonii*. However, no populations, other than those already recorded, have been found in this region, although it seems possible that the intensive shifting agriculture which has taken place, particularly along the southern portions of the littoral, may have caused some elimination.

It was suggested [Kirkia 3: 36 (1963)] that *E. johnsonii* might be best considered as a variety of *E. knuthii*; however, in view of the disjunct and discrete distributions of the two taxa, together with the degree of discontinuity in those characters by which they are distinguished, it seems that subspecific rank is a more correct assessment of the taxonomic situation.

The subspecies appear to differ only in habit and the number of angles to the branches. In subsp. *knuthii* 3–4-angled branches (rarely 5-angled) are produced from a rhizomatous mass of roots, usually with a large main tuber, often with plantlets arising at some little distance from the parent plant; individuals sometimes occupying an area 60 cm or more in diam. Subsp. *johnsonii*, on the other hand, is normally a solitary plant with relatively few 2–3-angled branches (only one plant has been found with 3–4-angled) arising from a single large tuberous root, with only rarely a tendency towards a rhizomatous habit.

Subsp. *knuthii*

Euphorbia knuthii Pax in Bot. Jb 34: 83(1904).—N.E.Br. in Fl. Cap. 5(2): 363(1915).—Phillips in Flow. Pl. S. Afr. 9: t.348(1919).—Burt Davy, Fl. Pl. & Ferns Transv. & Swazil. 2: 296(1932).—White, Dyer & Sloane, Succ. Euphorb. 2: 732(1941).—Jacobsen, Handb. Succ. Pl. 1: 445(1960) et Sukk. Lexikon: 193(1970).

Type: MOÇAMBIQUE, Ressano Garcia, Schlechter 11949 (G; PRE;).

The distribution of this subsp. is now known to be rather more extensive than was originally thought. Plants are common and widespread in the Delagoa



FIG. 12.

Plant from Komatipoort with
numerous tuberous roots.

Leach 13112

Plant from "Maputoland" showing
development of rhizomes

Leach & Bayliss 11943

Euphorbia knuthii* subsp. *knuthii



FIG. 13.

Specimen from type locality
showing tendency towards a
rhizomatous habit.

***Euphorbia knuthii* subsp. *johnsonii* *Leach* 11244**

Normal plants from type locality,
with simple tuberous roots.

Bay region of Moçambique, particularly in low-lying, black turf areas. In some of the extensive seasonal vleis between Boane and Catuane, dense populations occur, often in close association with equally large numbers of *Stultitia paradoxa* Verdoorn. Terrain characteristic of this "Maputoland" country extends into northern Zululand and, as is to be expected, subsp. *knuthii* appears to be equally plentiful in that area to as far south as Mkuse. The more inland extension of its distribution appears to be restricted to the Transvaal, where some rather small and scattered colonies are to be found more or less along the Crocodile river valley, to as far west as Kaapmuiden.

Moçambique; LM Lourenço Marques Distr., between Moamba and Guija, *Torre* 6630 (PRE); between Moamba and Magude, *Torre* 7327A (LISC); near Motaze, *Torre* 7209 (LISC); 21 km N of Moamba, 3–5-angled, *Leach & Bayliss* 11749 (K; LISC; PRE; SRGH); Ressano Garcia, fl. 27.xii.1897, *Schlechter* 11949 (G; PRE); near Moamba, *Mendonça* 1550 (LISC), *ibid.* *Torre* 7942 (LISC); between Moamba & Boane, *Torre* 7938 (LISC); between Boane & Marracuene, hort. Lourenço Marques, *E. de Sousa* 80 (LISC; PRE); near Lourenço Marques, *van Balen* s.n. in Nat. Herb. 8030 (PRE), *ibid.* *Bodley* 579 (PRE); near Boane, hort. Nelspruit, fr. Jan. 1963, *Leach & Bayliss* 11029 (BR; G; LMA); between Umbeluzi & Bela Vista, *Pedro* 3125 (LMA); between Umbeluzi & Goba, *Torre* 1848 (LISC); "Maputo", *Barbosa* 583 (LISC); between Boane & Catuane, *Leach & Bayliss* 11943 (SRGH); 22 km N of Catuane, *Leach & Bayliss* 11936 (K; LMA; PRE; SRGH); near Catuane, *Mendonça* 2985 (LISC), *ibid.* *Torre* 1915 (LISC).

S. Africa, TRANSSVAAL; 2531 (Komatipoort): Hectorspruit (-BC), hort. Salisbury, fl. & fr. 24.iii.1961, *Leach* 10756 (PRE); Komatipoort (-BD), st. 27.viii.1965, *Leach* 13112 (G; PRE; SRGH), *Van der Merwe* E18 (PRE); Nelspruit Distr., Kruger Nat. Park, fl. Jan. 1953, *Van der Schijff* 1802 (PRE).

NATAL; 2632 (Bela Vista): Ndumu Game Reserve (-CD), 4.xi.1969, *Moll* 4290 (PRE), *Ward* 3115 (PRE). 2732 (Ubombo): Mkuze Br., Candover-Nongoma Rd. (-CA), fl. & fr. 13.xi.1968, *Venter* 5202 (PRE); Ingwavuma Distr., Opondwini Riv. (-A), *Hardy* 1273 (PRE), *Strey* 4657 (PRE); ±29 km from Otoberini pont on Ingwavuma road, *Edwards* 2926 (PRE).

Swaziland; 2631 (Mbabane) Ubombo Mtns., near Stegi, 8.iii.1935, *Keith* s.n. (PRE).

This specimen probably belongs here although a measure of uncertainty exists as the plant is sterile. However, Capt. Keith is known to have cultivated numbers of indigenous plants in his garden near Stegi and it is suspected that the record may refer to one of these; moreover, despite intensive collecting throughout Swaziland by Professor H. Compton, in addition to the investigation of apparently likely localities by Col. R. D. Bayliss as well as by the author, the species has not again been recorded from the territory.

Subsp. *johnsonii* (N.E.Br.) Leach, stat. nov.

Euphorbia johnsonii N.E.Br. in Fl. Trop. Afr. 6(1): 511(1911).—White, Dyer & Sloane, Succ. Euphorb. 2: 736(1941).—Jacobsen, Handb. Succ. Pl. 1: 444(1960) et Sukk. Lexikon: 192(1970), p.p. excl. distrib. Malawi.—Leach in Kirkia 3: 34(1963).

Type: MOÇAMBIQUE, Manica e Sofala Distr., Cherinda, *W. H. Johnson* s.n. (K).

In contrast to the rather extensive distribution of the typical subsp. that of subsp. *johnsonii* appears to be restricted to a relatively short stretch of the coastal plain between the Savé and Buzi rivers.

Moçambique; MS: Manica e Sofala Distr. between the Buzi and Sofala rivers, near Ampara and Gorongoza Riv., fl. 29.viii.1961, *Leach* 11240 (K; LISC; PRE; SRGH); near Cherinda, fl. 31.viii.1961, *Leach* 11244 (G; K; LMA; PRE; SRGH).

The sketch, by A. F. Gomes e Sousa, of a plant from near Nampula, which White, Dyer & Sloane, l.c., very tentatively suggest may represent *E. johnsonii*, does in fact depict a plant in many ways quite different. The writer has been unable to rediscover plants corresponding to this figure at any locality in N. Moçambique; its identity consequently remains obscure although it appears to have little connection with *E. knuthii*.

E. knuthii was considered by N. E. Brown (Fl. Cap. l.c.) to be related to *E. squarrosa* Harv. and *E. schinzii* Pax. However, although sometimes having a somewhat similar appearance, it is considered that the connection with the latter species is, in fact, rather remote. *E. schinzii* belongs in a numerous and widespread group which includes among its common characteristics: a barely or only very shortly exserted, obtusely lobed capsule and more or less ellipsoid, verrucose seeds; whereas *E. knuthii* appears to find its affinities with such species as *E. squarrosa* and *E. stellata* Willd., in which the more deeply lobed, more acutely angled capsule with its smooth, subglobose seeds is far exserted from the involucre on a long curved pedicel. It seems worthy of note that these characters are shared also, to a greater or lesser extent, by a number of tropical and subtropical species, some of which, e.g. *E. grandidens* Haw., *E. evansii* Pax and *E. confinalis* R. A. Dyer, are found in the same geographical area as *E. knuthii*.

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OBSERVATIONS ON THE STAINING OF PECTIC SUBSTANCES AS EXTRACTS AND IN THE TRANSFUSION TRACHEIDS OF *WELWITSCHIA*

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ABSTRACT

A series of staining-time sequences was used to stain extracts of pectin and pectic acid with alkaline hydroxylamine-ferric chloride, specific for these substances, in an attempt to find an improved, reproducible and, if possible, a quantitative staining technique at the electron microscope level. The unfortunate heterogeneity and variability in composition of such pectic preparations made this impossible.

However, good differential staining was obtained using the stain *in vivo* on *Welwitschia mirabilis* one-year-old leaf sections. The distribution of the pectic substances within the cell walls of differentiating transfusion tissue, particularly of transfusion tracheids, was studied.

UITTREKSEL

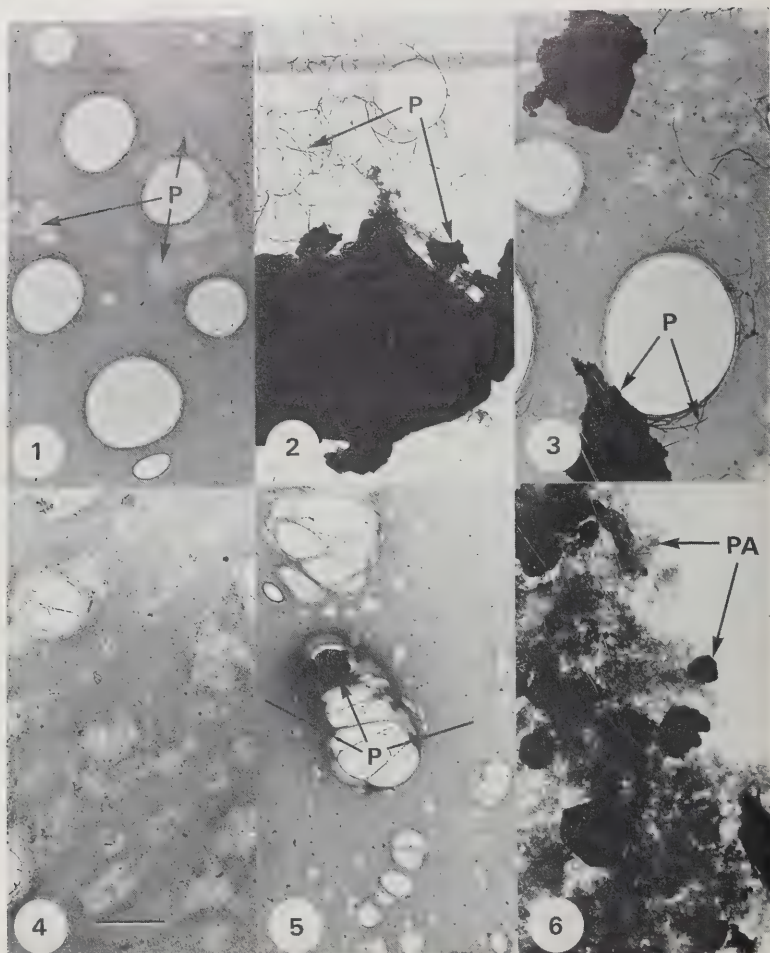
WAARNEMINGS OP DIE KLEUR VAN PEKTIËSE STOWWE AS EKSTRAKTE EN OOK IN DIE TRANSFUSIE-TRAGEÏEDE VAN *WELWITSCHIA*

In 'n poging om 'n verbeterde, herhaalbare en moontlik kwantitatiewe kleurtegniek vir pektiese verbindings in plantweefsel op elektron mikroskopiese vlak daar te stel, is 'n aantal kleur- en tydsekwensies met pektien en pektiënsuur in samehang met alkaliese hidroksielamien-ferrichloride uitgevoer. Die variasie in en heterogene aard van die samestelling van die pektiese preparate het egter die pogings grotendeels verrydel.

Goed-gedifferensieerde kleuring is egter *in vivo* verkry met ultradun sneë van eenjarige blare van *Welwitschia mirabilis*. Die verspreiding van pektiese stowwe in die selwande van die differensierende transfusie-weefsel, vernameklik die transfusie-trageïede, is bestudeer.

INTRODUCTION

A number of attempts have been made to find a stain specific for pectic substances and which also makes possible their histochemical localisation with the electron microscope. The heavy metal dye, ruthenium red, often used in light microscopy as a pectin stain, does not have the required specificity (Kertesz, 1951). Gee, Reeve and McCready (1959) found that alkaline hydroxylamine-ferric chloride was specific for pectic substances and used this stain in conjunction with the light microscope. The insoluble iron complex formed with the reactive methoxy groups of pectin is also electron dense, a property required for stains used in electron microscopy. Therefore this stain was tried at the electron microscope level as well (Albersheim *et al.*, 1960, 1963; Bornman *et al.*, 1969). Albersheim *et al.* used a prefixation staining technique on onion root tips, while Bornman *et al.* stained after fixation and sectioning of abscission zone tissue in *Coleus* and *Gossypium* petioles.



FIGS. 1-6.

Fig. 1. Pectin (P) dusted onto formvar-coated grid. STAIN (control): Soln. B (0,75 min.) + Soln. C (2 min.). Pectin particles unstained. Fig. 2. Pectin (P) dusted. STAIN: Soln. A (15 min.) + Soln. B (0,75 min.) + Soln. C (5 min.). Pectin stained intense black. Fig. 3. Pectin (P) dusted. STAIN Soln. A (2 min.) + Soln. B (0,75 min.) + Soln. C (1 min.). Pectin stained intense black. Fig. 4. Pectin (P) incorporated into formvar coating. STAIN (control): Same as in Fig. 1. Pectin particles unstained. Fig. 5. Pectin (P) incorporated. STAIN: Same as in Fig. 2. Pectin stained intense black. Fig. 6. Pectin acid (PA) dusted. STAIN: Same as in Fig. 3. Particles stained intense black.

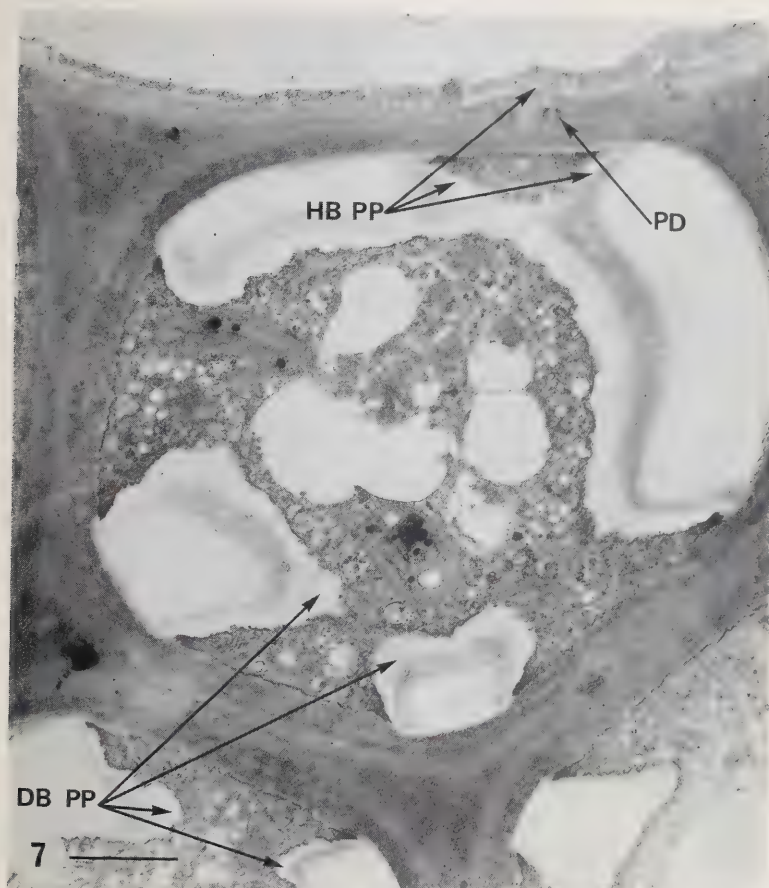


FIG. 7.

TS through transfusion tracheid. STAIN (control): Soln. B (0,5 min.) + Soln. C (1,5-2 min.). There is no real difference in stain intensity between compound middle lamella and cytoplasmic contents. DB PP, bordered pit pair; HB PP, blind pit; PD, plasmodesma.

This paper reports firstly on attempts to stain extracts of pectic acid and pectin differentially at the electron microscope level by using different staining-time sequences. It was hoped that, in the results of the study, there would be found a basis either for a quantitative stain for pectic substances *in vivo*, or a method of staining which would give more reproducible results for pectic

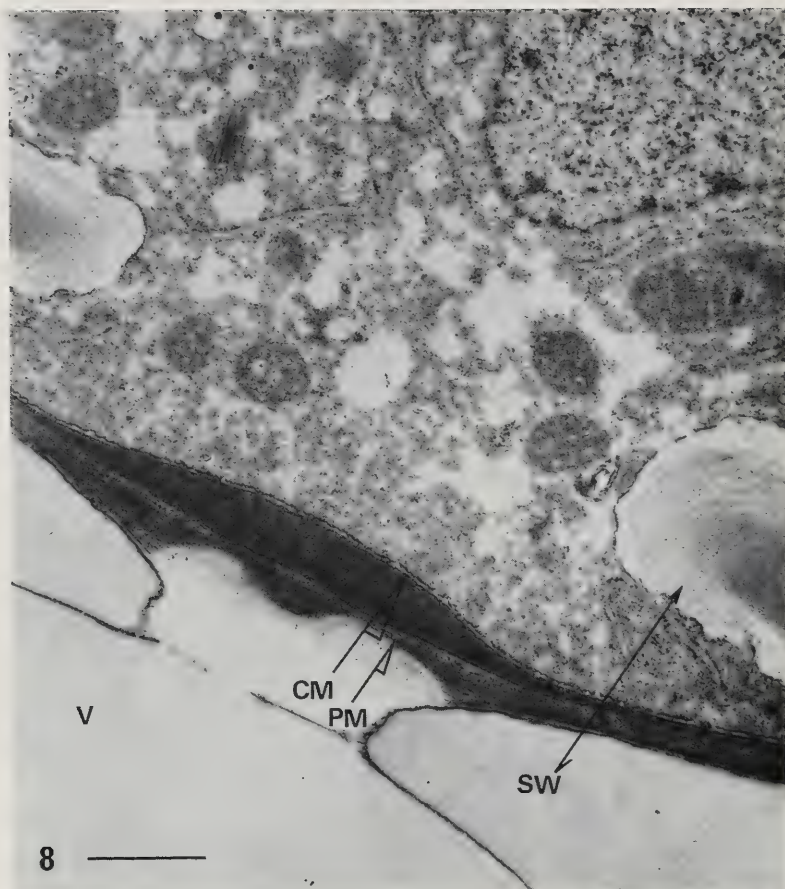


FIG. 8.

TS through pit region between two transfusion tracheids. STAIN: Soln. A (15 min.) + Soln. B (0,5 min.) + Soln. C (1,5-2 min.). Compound middle lamella (CM) stained intensely; pit membrane (PM) very lightly stained as a result of pectic substance breakdown. Very few pectic substances in secondary wall (SW) of younger transfusion tracheid but none in secondary wall of older cell. V, vacuole.

substances in plant tissue than those obtained hereto. Secondly, *Welwitschia* leaf sections were also stained in order to test the specificity of the hydroxylamine-ferric chloride stain *in vivo*, and a subsequent examination of the distribution of pectic substances in the differentiating transfusion tracheids was made.

MATERIALS AND METHODS

Samples of powdered pectic acid and *Citrus decumana* pectin extracts, as well as *Welwitschia* one-year-old leaf sections, were stained. *Staining solutions:* (Albersheim *et al.*, 1960)

Solution A: Alkaline hydroxylamine (equal volumes of 14 g NaOH per 100 ml and 14 g $\text{NH}_2\text{OH} \cdot \text{HCl}$ per 100 ml) 60% with respect to ethanol.

Solution B: 95% ethanol: conc. hydrochloric acid (10:1). Wash to acidify.

Solution C: 10% ferric chloride (anhydr.) solution in 60% ethanol containing 0,05 N HCl. Centrifuged before use.

Wash: Distilled water.

Staining procedure

Three different combinations of staining times were used for each specimen (Table I), and examined under the electron microscope.

Controls were treated with solutions B and C only, the basic hydroxylamine treatment being omitted.

The staining sequences of the *Welwitschia* sections had to be modified slightly as a result of disintegration of the copper grids in Solution C.

TABLE I
Different staining sequences used on specimens mounted in various ways on electron microscope grids*

METHOD: (i)–(iii) Pectin, Pectic Acid (iv) <i>In vivo</i>	STAINING TIMES (MIN.)			
	Solution A	Solution B	Solution C	
(i) Dusted (Ni grids)	— 15 10 2	0,75 " " "	2 5 2 1	Control
(ii) Spread (Ni grids)	— 15 10 2	0,75 " " "	2 5 2 1	Control
(iii) Incorporated (Ni grids)	— 15 10 2	0,75 " " "	2 5 2 1	Control
(iv) Leaf Sections (Cu grids)	— 15	0,5 "	1,5–2 "	Control

* Wherever possible, nickel (Ni) grids were used. However, when the leaf sections which had already been mounted on copper (Cu) grids were being stained, the grids tended to disintegrate after about 2 minutes in the ferric chloride solution. The uranyl acetate/lead citrate staining of these sections prior to their being stained for pectin probably accelerated this disintegration.



FIG. 9.

TS through two transfusion tracheids (TT) surrounded by four other mesophyll cells (MC). STAIN: Same as in Fig. 8. Breakdown of pectic substances in pit regions of compound middle lamella (CM). Primary wall (PW) of mesophyll cells still completely intact and distinguishable from compound middle lamella. P, plastid; M, mitochondrion. This stage is more advanced than in Fig. 8.

The extracts of pectic substances were applied to the grids either on or in a coating of formvar (0.3% in ethylene dichloride) in three different ways: by dusting formvar-coated grids with finer particles of pectic compound, by spreading a drop of the pectic substances suspended in 80% ethanol onto the coated



FIG. 10.

TS through two transfusion tracheids. STAIN: Same as in Fig. 8. Distribution of pectic substances (PS) in different layers of cell wall clearly illustrated; pit membrane (PM) is on side nearest the older transfusion tracheid and plasmalemma (PL) of younger cell is still intact. The dark specks are probably from the disintegrating copper grid. Stage of development approximately the same as in Fig. 9.

grid, or by incorporating the extracts into the formvar solution before using this suspension to coat the grids.

Good sections of one-year-old *Welwitschia* leaf tissue on copper grids which had already been stained with uranyl acetate/lead citrate were available. Only

those on which the compound middle lamella was clearly visible were selected for further staining with the hydroxylamine-ferric chloride stain.

RESULTS AND DISCUSSION

Figures 1-3 illustrate a series of stain treatments on pectin dusted onto

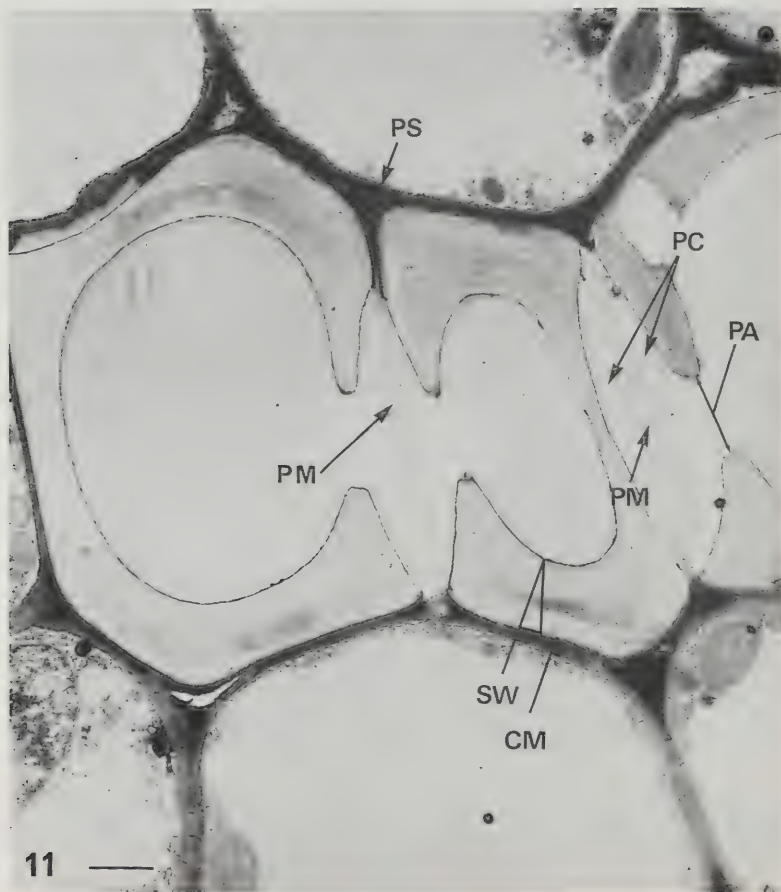


FIG. 11.

TS through transfusion tracheids at most advanced stage of differentiation. STAIN: Same as in Fig. 8. These cells have no cytoplasmic contents, neither are there any pectic substances in the pit membranes (PM). Darkly stained pectic substances (PS) are present in compound middle lamellae (CM) when adjacent to mesophyll cells. PA, pit aperture; PC, pit cavity; SW, secondary wall.

formvar-coated grids. No staining can be seen in the control (Fig. 1) whereas the pectin particles and fibres in the full treatments (Figs. 2 and 3) appear an intense black. There is apparently no difference in intensity of staining between the longest and shortest treatments.

Pectin particles incorporated into the formvar coating are shown in Figs. 4 and 5. Here, too, the control pectin is unstained while the fully stained pectin, at the periphery of a hole in the formvar membrane, is an intense black.

In Fig. 3 (pectin) and Fig. 6 (pectic acid) both groups of pectic substance have been dusted onto formvar and stained with the shortest treatment. In pectic acid, there is very little, if any, methylation of the carboxyl groups (Salisbury and Ross, 1969), and so the amount of stain complex formed would be expected to be proportionally less than the amount formed with pectin, which has a much greater degree of esterification of carboxyl groups (Bonner and Varner, 1965). However, it is difficult here to see any difference in intensity of staining between the two groups of pectic substances. This could be as a result of a certain degree of methylation having taken place in the pectic acid sample.

In all methods and staining sequences used on the extracted pectic substances, the same rather inconclusive results were obtained. The fundamental problem proved to be the unreliability in composition of the pectic preparations themselves.

The alkaline hydroxylamine-ferric chloride treatment of the leaf sections resulted in good differential staining of the compound middle lamellar pectic substances, even though an impression of the effect of different staining times on intensity of staining could not be gained because of the rapid disintegration of the copper grids. In *Welwitschia* leaf tissue, the distribution of pectic substances in the walls of transfusion tracheids, especially in the pit regions, during some stages in their differentiation is illustrated in Figs. 7–11. Transfusion tracheids form a specialized transfusion tissue when in association with parenchyma cells and so far have been found only in the leaf tissue of some gymnosperms and in leaf, root and stem tissue of *Welwitschia* (Gilliland *et al.*, 1971).

FIGS. 7–11.

Transfusion tracheids in leaf of one-year-old *Welwitschia* seedling. Bars represent 1 μm .

Figure 7, the control, shows a young transfusion tracheid which has formed bordered pit pairs where it lies adjacent to other transfusion tracheids, and a blind pit where adjacent to a mesophyll cell. There is no great distinction between the intensity of staining of the compound middle lamella and that of the cytoplasmic cell contents.

Figures 8, 9, 10 and 11 are fully stained sections of transfusion tissue showing stages of increasing maturity of transfusion tracheids. The pectic substances of the compound middle lamellae have become much more intensely stained

than the cytoplasmic contents (if still present) and the control wall pectic substances of Fig. 7. Pectic compounds were present in large quantities in the compound middle lamellae and were densely accumulated in the intercellular regions at the junctions of cells. They were also present, but very sparsely distributed, in the secondary walls of transfusion tracheids at the earlier stages of differentiation.

During maturation of a transfusion tracheid, breakdown of pectic substances (presumably by hydrolytic enzymes) in a pit region of the compound middle lamella begins from the side immediately adjacent to the cell lumen and gradually progresses outwards (Figs. 8, 10, 11). The compound middle lamella broadens noticeably in the pit region (Fig. 8). If the pit forms part of a pit-pair between two transfusion tracheids, breakdown commences from the side of the older wall and probably is completed as the younger cell ages (Figs. 8, 10). Eventually all pectic compounds in the pit membrane between the two cells disappear (Fig. 11). On the other hand, if the pit is a blind pit, e.g. in a transfusion tracheid wall opposite a mesophyll cell as in Fig. 9, only partial breakdown in the wall between the two cells takes place and the primary wall of the mesophyll cell, in which the pectic substances are less dense, remains intact, seemingly unaffected by the agent of pectic substance breakdown.

If this agent is a type of enzyme (as is suggested by the pattern of breakdown), its synthesis in a transfusion tracheid would be possible only as long as the cytoplasmic contents remain functional. In a situation as is present in Fig. 9, therefore, it is difficult to imagine that the older transfusion tracheid is capable of synthesizing further the enzymes which will continue the breakdown process in the compound middle lamella. It seems feasible that, at this stage, there may either be a delay in the process until breakdown commences from a younger transfusion tracheid on the other side of the cell wall, or, if the other cell is a mesophyll cell, there will be no further breakdown of pectic substances at all.

CONCLUSION

The usefulness of the hydroxylamine-ferric chloride stain in histochemical localisation of pectic substances at the subcellular level is obvious. However, this technique must still be greatly refined before it can be used as a reliable method for the quantitative histochemical determination of these compounds in plant material.

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THE FLAGELLA OF *CYANOPHORA PARADOXA* KORSCH

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ABSTRACT

Both flagella of *Cyanophora paradoxa* are tinsel, resembling the Cryptophycean rather than the Dinophycean flagella. The organism appears to be an intermediate between the Cryptophyceae and the Dinophyceae.

UITTREKSEL

DIE FLAGELLA VAN *CYANOPHORA PARADOXA* KORSCH.

Beide flagella van *Cyanophora paradoxa* is van die flikkertipe en kom meer ooreen met die flagellum van die Cryptophyceae as met dié van die Dinophyceae. Die organisme is skynbaar intermediêr tussen die twee phyla.

INTRODUCTION

Cyanophora paradoxa Korschikoff is a unicellular alga traditionally classified into the Cryptophyceae (Family Cryptomonadineae). It is ovoid, truncated anteriorly and rounded posteriorly; the dorsal surface is convex, while the ventral surface is traversed by a longitudinal groove. The organism is 12-15 μm long, and 6-9 μm wide. Two trailing flagella inserted at approximately 120° , emerge in separate flagellar pits, and are 3-12 μm long (Figs. 1 & 2).

Originally classified by Korschikoff (1924), its affinities with the Cryptophyceae have been questioned (Korschikoff, 1941; Pringsheim, 1964). Mignot *et al.*, (1969), studying the ultrastructure, found Dinophycean and Cryptophycean features, indicating that the organism is an intermediate between the Dinophyceae and Cryptophyceae. The most conclusive Dinophycean feature found was the membrane-bound vesicles containing thecal plates, situated below the plasmalemma.

The ultrastructure of the flagellar surface was studied to see whether the flagella possessed Dinophycean or Cryptophycean features. The structure of the flagella differs markedly in the two groups. The Cryptophyceae have two tinsel flagella; the Dinophyceae have one whiplash flagellum while the other has a lateral expansion of the flagellar sheath ending in a striated strand. (Hibberd *et al.*, 1971; Leadbeater and Dodge, 1966.)

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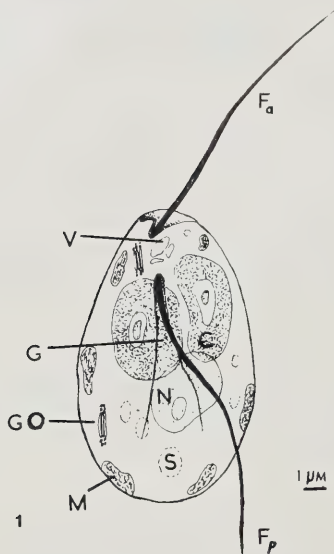


FIG. 1.

Whole cell of *Cyanophora paradoxa*. C = cyanelle containing thylakoids; N = nucleus; S = starch grain; V = pulsating vacuole; GO = Dictyosomes; M = mitochondrion; F_a = anterior flagellum; F_p = posterior flagellum; G = flagellar groove. (After Mignot *et al.*, 1969).



FIG. 2.

A scanning electron micrograph of *C. paradoxa*. G = flagellar groove; F_a = anterior flagellum; F_p = posterior flagellum. $\times 5\,500$.

MATERIALS AND METHODS

C. paradoxa was sub-cultured from the collection of the Botany Department, University of the Witwatersrand, and grown in Bolds 3N Bristols nutrient solution (Starr, 1966), using normal daylight illumination.

Two methods of fixation were used.

- (a) Cells were exposed to 1–2% O_3O_4 vapour for a few minutes, and washed in distilled water (modified from Loiseaux and West, 1970).
- (b) Cells were fixed in 1–2% O_3O_4 in Millonig's phosphate buffer at pH 7.3 for one hour at 4°C, dried onto grids, and washed in distilled water (Bradley 1965, 1966).

Two methods of preparation were used.

- (a) Fixed cells were dried onto carbon-stabilized formvar grids, shadowed with carbon-platinum and gold-palladium at angles of 30–45°, and viewed under a Siemens Elmiskop I Electron Microscope. (Heath *et al.*, 1970).
- (b) Fixed cells were pipetted onto aluminium rivets, the rivets submerged in liquid nitrogen, vacuum dried for 10 hours at 5×10^{-5} torr, and gold coated. They were examined under a Cambridge Stereoscan Electron Microscope (Edwards and Black, 1971).

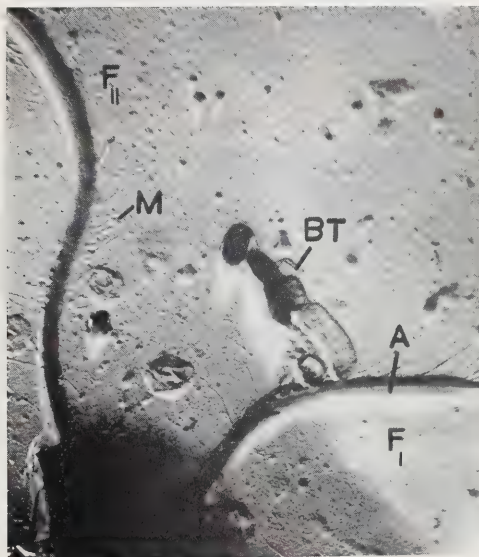


FIG. 3.

Part of a cell showing both flagella to be tinsel. M = mastigonemes; A = axoneme; F₁ and F₁₁ = flagella; BT = bacterial contamination. $\times 16\ 000$.

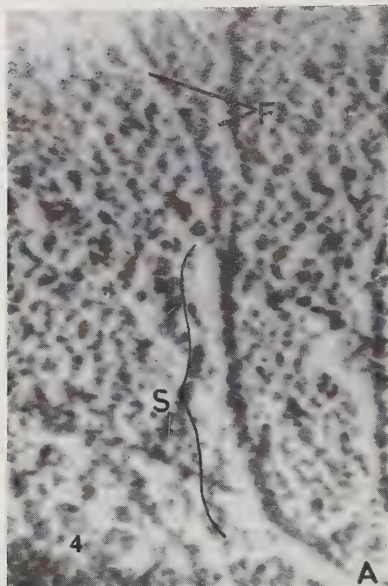


FIG. 4.

Proposed structure of a mastigoneme. S = main shaft; F = terminal filaments; A = axoneme.
 $\times 320\ 000$.



FIG. 5.

Tip of a flagellum showing tapering of the terminal axoneme into a "beak". A = axoneme;
 T = "beak"; M = mastigonemes. $\times 80\ 000$.

RESULTS AND DISCUSSION

Both flagella were tinsel, with a unilateral row of mastigonemes on both sides of the axoneme (Fig. 3). The mastigonemes appeared to have the same structure as found in the Cryptophyceae and Dinophyceae viz. a main shaft attached to the axoneme, and terminating in one to three filaments (Hibberd *et al.*, 1971) (Fig. 4). The axoneme tips often had a characteristic "beaked" structure (Fig. 5). No evidence was found of the Dinophycean flagellar structure.

This further supports the claim that the organism is an intermediate, which is of importance in algal phylogeny.

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A NEW VARIETY OF *ALOE* FROM NAMAQUALAND

J. J. LAVRANOS

ABSTRACT

A new variety of *Aloe krapohlina* Marloth is described and compared to the typical form of the species.

UITTREKSEL

'N NUWE *ALOE* VARIËTEIT VAN NAMAKWALAND.

'n Nuwe *Aloe krapohlina* Marloth variëteit word beskryf en met die tipiese vorm van die soort vergelyk.

DESCRIPTION AND DISCUSSION

Aloe krapohlina Marloth var. **dumoulinii** Lavranos var. nov. a typo habitu polycephalo, foliis minoribus, incurvatis, floribus ventricosis satis differens.

Type Material: SOUTH AFRICA; Cape Province; 2816 DA (Namaqualand). On bare, windswept, white quartzite hills S.E. of Alexander Bay, alt. appr. 150 m., Lavranos *et* Butler 8777, coll. 28 Aug. 1971 (PRE, Holotype.)

The writer's attention was first drawn to this beautiful plant by Mr. J. P. Swanepoel of Somerset West in the Cape. It had been collected by Mr. J. Dumoulin, Director of the Hester Malan Wild Flower Reserve of Springbok, Namaqualand, a few miles S.E. of Alexander Bay, growing on bare quartzite ridges in conditions of extreme aridity. It was at first thought that it might represent nothing more than a local growth form of *A. krapohlina*. This species varies very considerably in the size of all its parts except the flowers but it invariably has arcuate-erect leaves, unspotted even in the minutest seedlings and remains solitary unless damaged, when it may produce 2 rosettes by division.

In late August 1972 the author, in the company of Mr. R. A. Butler and Mr. J. Dumoulin visited the type locality of the new variety. Large numbers of plants were found and this made it possible to ascertain that the characters whereby they differed from typical *A. krapohlina* were consistent throughout the population of several hundred plants examined.

It was found that about one half of these plants have more than one and up to fifteen rosettes which are apparently produced both by division and by offsetting. Of these many-headed specimens, not a few are lodged in deep clefts among the rocks, where they cannot have been damaged and the existence of

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many rosettes to each plant seems, on available evidence, to be a stable character of this population.

Moreover, individual rosettes are smaller than in even the least robust forms of *A. krapohlina* and the leaves much shorter, distinctly deltoid and strongly incurved, even in the turgid state. The peduncle is not more than 15 cm long, the racemes sub-lax, with 12–18 flowers.

The pedicels are 12–15 mm long (against about 20 mm) and the perianths, 25–27 mm long (as against 30–35 mm), are distinctly ventricose, measuring 6–7 diam. over the ovary and 8–9 mm at their middle, being restricted to 4 mm at the mouth.

The constancy of these characters would appear to indicate genetic homogeneity within the population examined. It consequently seems advisable to recognise it as a discrete variety of *A. krapohlina* and the writer has much pleasure in naming it after its discoverer, Mr. J. Dumoulin and his son Johannes.



FIG. 1.

Aloe krapohlina var *dumoulinii*. Flowering, single-headed specimen showing the distinctive leaf form; Photo: Botanical Research Institute.

ACKNOWLEDGEMENTS

The author is much indebted to the Department of Nature Conservation of the Cape Provincial Administration for their help and co-operation over many years.

The Chief, Botanical Research Institute, Pretoria for the use of the facilities of the National Herbarium.

Mr. and Mrs. Jan Dumoulin for guiding him to the habitat of the variety here described.

STUDIES ON THE SOUTH AFRICAN BULBOUS LILIACEAE: 4. A NEW SPECIES OF *LEDEBOURIA* FROM SOUTH WEST AFRICA

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ABSTRACT

A new species is described from the Gobabis district of South West Africa. The diploid chromosome number is 40.

UITTREKSEL

STUDIES VAN DIE BOLDRAENDE LILIACEAE IN SUID-AFRIKA: 4. 'N NUWE SOORT *LEDEBOURIA* VANAF SUIDWES-AFRIKA
'n Nuwe soort *Ledebouria* is uit die Gobabis distrik van Suidwes-Afrika beskryf. Die diploïede chromosoom getal is 40.

Only three species of *Ledebouria* were recognised from South West Africa by Jessop (1970). These are *L. cooperi*, *L. revoluta* and *L. undulata*. In 1970, living material of a fourth species was collected by Mr. H. R. Tölken in the Gobabis district. This material flowered in Grahamstown in summer 1971/2.

***Ledebouria scabrida* Jess., sp. nov., *L. revolutae* (L.f.) Jess. affinis, sed foliis scabridis et bulbo in collum sursum producto.**

Bulbi 30-40 mm longi, 35-40 mm lati, in collum sursum producti, cinerei vel brunnei. Folia lanceolata, 80-170 mm longa, 20-30 mm lata, patentes vel erecto-patentes, rosulata, scabrida sursum, ubi lacerata fila plurima non exhibentes. Pedunculi solitarii, c.100 mm longi, floribus 25-30. Bractee binatae, infima 1-1,5 mm longa. Pedicellii patentes vel erecto-patentes, 5-7 mm longi. Perianthii segmenta pallida, vitta dorsali roseo-brunneo, ad apicem tumidi, c.5 mm longi, sub medio reflexi. Filamenta rosea, adnata, c.4 mm longa. Antherae roseae. Ovaria viridia, 1,5 mm longa. Styli albi, 2,5 mm longi.

Type: SOUTH WEST AFRICA; Epukiro (2119), Sturmveld, Tölken s.n., December 1970 (GRA, holo.) (Fig. 1).

Bulbs 30-40 mm long, 35-40 mm broad, produced apically into a slightly fleshy neck c.25-35 mm long. Outer scales membranous, grey to brown, not marked with red or purple. *Leaves*: 3 or 4, lanceolate, 80-170 mm long, 20-30 mm broad, spreading to erect-spreading, rosulate (not distichous), marked with

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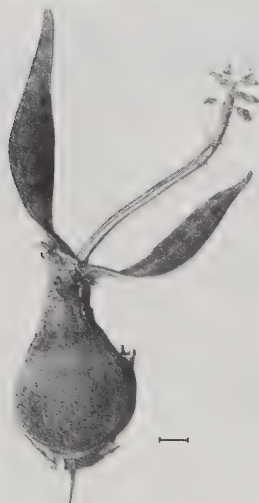


FIG. 1.

Holotype of *Ledebouria scabrida* sp. nov. (Tölken s.n.) Scale is 10 mm.

darker green patches or groups of dots on the upper surface, not producing threads when torn. Upper surface scabrid. Lower surface smooth. Margin ciliate. *Peduncle* solitary, c.100 mm long, with 25–30 flowers. *Bracts* paired, the lower 1–1,5 mm long. *Pedicels* spreading to erect-spreading, 5–7 mm long. *Perianth segments* pale, with a light pinkish brown dorsal stripe, swollen at the apex, c.5 mm long, reflexed just below the middle. *Filaments* pink, adnate to the perianth segments, c.4 mm long. *Anthers* pink. *Ovary* green, 1,5 mm long. *Style* white, 2,5 mm long.

Occurs on the margin of calcareous depressions, with *Acacia mellifera* subsp. *detinens*. Flowers during summer.

Diploid chromosome number (based on three cells) is 40.

Although there is only one other specimen known of this species, it is possible that *Drimiopsis papillosa* Dint. (Fedde. Repert. 17: 189; 1921) is synonymous. Dinter cited his material as "H.: Etemba, in Massen in der grossen Kalkpfanne, Dtr. 3298; Eahero, Dtr.". This material has not been located. The leaves are described as being covered on the upper surface by large "glitzernden" papillae. He also remarked:—"Möglicherweise handelt es sich aber auch hier nur um eine neue *Scilla*." There is no indication in the description that the material included flowers, which would have been necessary for a generic identification.

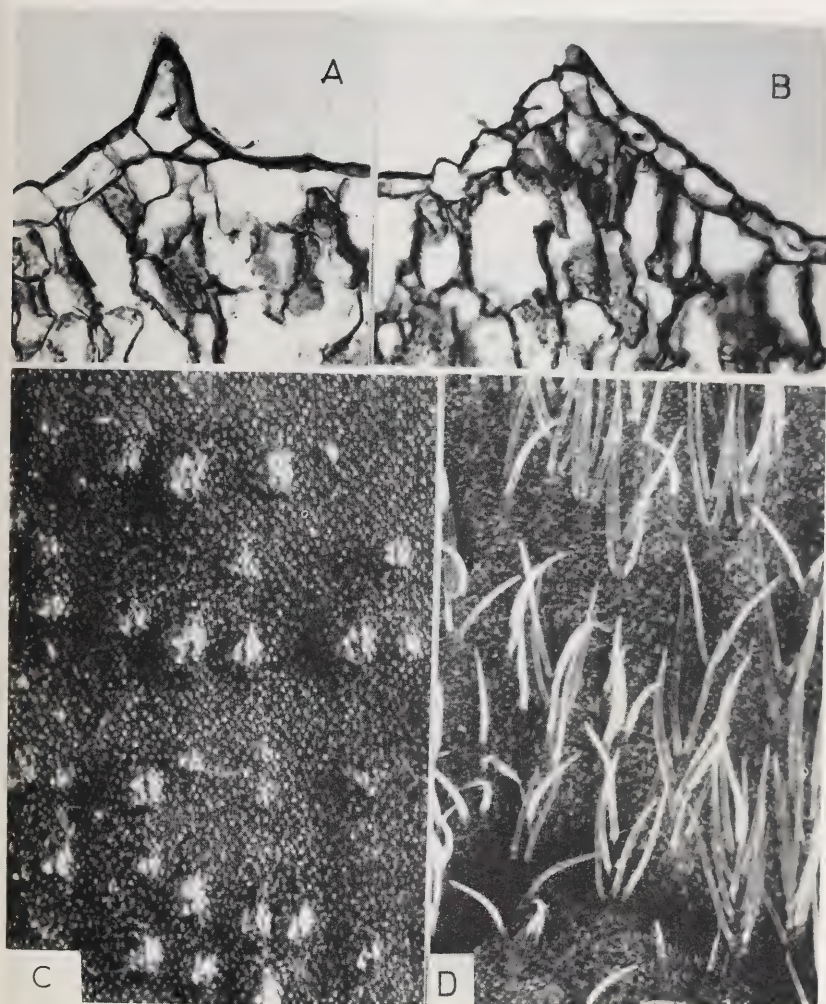


FIG. 2.

A. & B. Transverse sections through leaf of *L. scabrida* to show projections, X90. C. Surface view of leaf of *L. scabrida*, X20. D. Surface view of leaf of *L. hypoxidioides*, X20.

The protuberances, giving the plant its scabrid character, are of interest as only one species of *Ledebouria* possesses more distinct trichomes—namely *L. hypoxidioides*. However, in *L. hypoxidioides*, which is known only from the Albany district of the Cape Province, they take the form of distinct somewhat silky hairs (Fig. 2).

In the key to the genus already published (Jessop, 1970:245) this new species would key out under lead '5' when it may be recognised by being distinctly scabrid on the ventral surface.

Specimens:

S.W.A.—2119 (Epukiro: Farm Sturmveld, *Tölken* s.n. (GRA); 2219 (Gobabis)?—"Gobabis", *Wernsdorff* 1 (M).

STUDIES IN THE GENUS *CERATIUM* SCHRANK WITH REFERENCE TO SPECIMENS COLLECTED IN THE AGULHAS CURRENT: 2. SECTION *MACROCERAS* OSTENFELD, SUBSECTIONS *ROBUSTA* KARSTEN AND *REFLEXA* (JÖRG.) REINECKE.

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ABSTRACT

The use of polar coordinates in the measurement of antapical horn curvature in Section *Macroceras* Ostf.* is discussed, followed by a taxonomic account of Subsections *Robusta* Karsten and *Reflexa* (Jörg.) Rein. with reference to specimens collected in the Agulhas current during I.G.Y. 1958.

UITTREKSEL

STUDIES IN DIE GENUS *CERATIUM* SCHRANK MET VERWYSING NA MONSTERS IN DIE AGULHASSTROOM VERSAMEL: 2: SEKSIE *MACROCERAS* OSTENFELD, SUBSEKSIES *ROBUSTA* KARSTEN EN *REFLEXA* (JÖRG.) REINECKE.

Die gebruik van polêre koördinate vir die meet van antapikale horing geboëheid in die Seksie *Macroceras* Ostf. word bespreek, gevolg deur 'n taksonomiese behandeling van die Subseksies *Robusta* Karsten en *Reflexa* (Jörg.) Rein. met verwysing na monsters wat gedurende die Internasionale Geofisiese Jaar, 1958, in die Agulhasstroom geneem is.

THE USE OF POLAR COORDINATES IN MEASURING ANTAPICAL HORN CURVATURE IN SECTION *MACROCERAS* OSTF.

INTRODUCTION: Species in the Subgenus *Orthoceratium* Sournia, in particular those belonging to Section *Macroceras*, are classified largely on the curvature of the antapical horns. Features of antapical horn curvature which vary in this Section are: the degree to which the horns are curved posteriorly, the nature of the recurvature forwards, which varies from gradual to abrupt, and the disposition of the anteriorly directed parts, ranging from spreading to almost parallel to one another and the apical horn. The antapical horns may lie in the same plane as the dorsiventrally flattened body, to almost at right angles ventral to the body plane.

The curvature of the antapical horns is a character difficult to express numerically. The only way to determine the curvature of the antapicals away

* The epithet of a subdivision of a genus must take the same form as the generic name, or that of a plural adjective agreeing in gender with the generic name. The section name *Macroceras* as originally given by Ostensfeld (1903) is thus correct, and is incorrectly spelled by Reinecke (1971). The specific epithet in *Ceratium macroceras* (Ehb.) Vanhoeffen is treated as a substantive, and the original spelling of Ehrenberg (1840) retained.

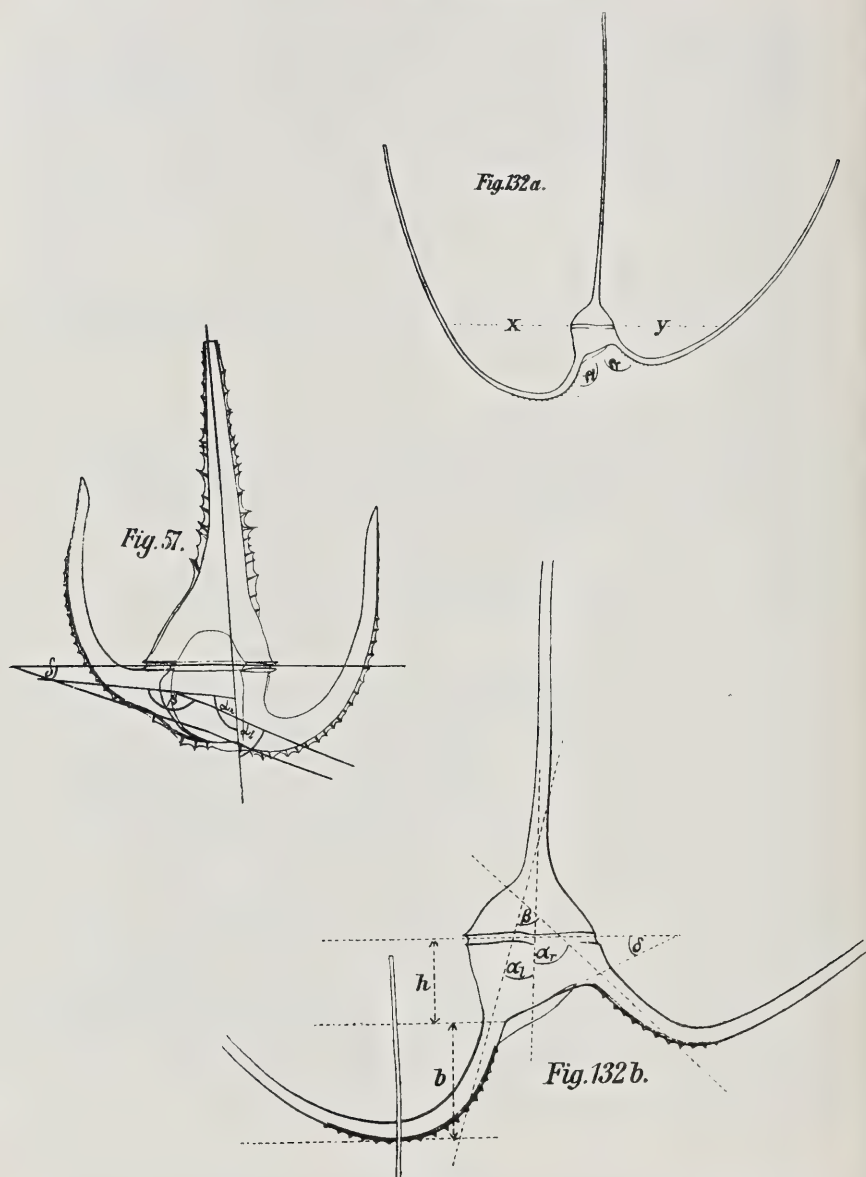


FIG. 1.
 Showing the system of lines and angles used by Jörgensen to measure the various features in *Ceratium*. (Jörgensen (1911) Pl. 3, fig. 57, Pl. 8, fig. 132 a, b.)

from the body plane is by means of a graduated fine adjustment focussing screw, and this method is not satisfactory. Jørgensen (1911) used a system of lengths and angles taken from camera lucida drawings to measure the two-dimensional curvature of the horns, but this was unsatisfactory because the points where some of the measurements were taken could not be well defined. (See Fig. 1.)

Yarranton (1967) devised a better method of measuring horn curvature by using polar coordinates. Placing camera lucida drawings of full dorsal or ventral aspects on polar coordinate graph paper, and taking as a base line, a line passing through the base of each horn, oriented parallel to a line joining the midpoints of the girdle at the edges of the cell, in the case of the apical horn, and perpendicular to the girdle line for the antapical horns, he measured the degree and radius coordinates along the middle of each horn. From these readings which gave second order curves in the taxa he studied, he calculated the parameters of the curves by the method of averages.

Yarranton examined four taxa, which he considered to be all members of "Section *Euceratium*": "*C. tripos*, *C. horridum*, *C. longipes* and *C. arcticum*". His results showed little variation within each taxon and sufficient discontinuity between the taxa to provide a satisfactory measure of the difference between the four.

METHOD: An attempt was made to classify specimens of Section *Macrocercas* from the Agulhas current NGY samples using Yarranton's method. The girdle was not used as a means of orientation, as in some specimens it is incompletely formed. On the camera lucida drawings, a line referred to as the posterior line, was drawn to pass through the antapical horns at their inception, immediately adjacent to the posterior margin of the hypotheca. Perpendiculars to this posterior line were drawn through these points of inception, and taken as base lines. Using polar coordinate graph paper, in this case marked in radius intervals approximately equivalent to $3\ \mu$ on the scale of the camera lucida drawings, the curvature of the antapical horns was measured in degrees at 5 radius unit intervals, (approximately $15\ \mu$), along the outer side of the horn, excluding lists if present. (See Fig. 2.)

For each taxon, the mean and standard deviation for the set of readings at successive $15\ \mu$ intervals were calculated, and graphs plotted to show the mean curvature of the antapical horns. The mean rate of change of direction of antapical horn curvature, measured in degrees over $15\ \mu$ intervals was also plotted. (See Fig. 4A-D.)

USE OF A POLYNOMIAL REGRESSION CALCULATION: Using the first ten pairs of polar coordinates from the $15\ \mu$ to the $150\ \mu$ radius, in a computerised polynomial regression calculation, the intercepts and regression coefficients for this part of the curve of the left antapical horn were determined for a selection of

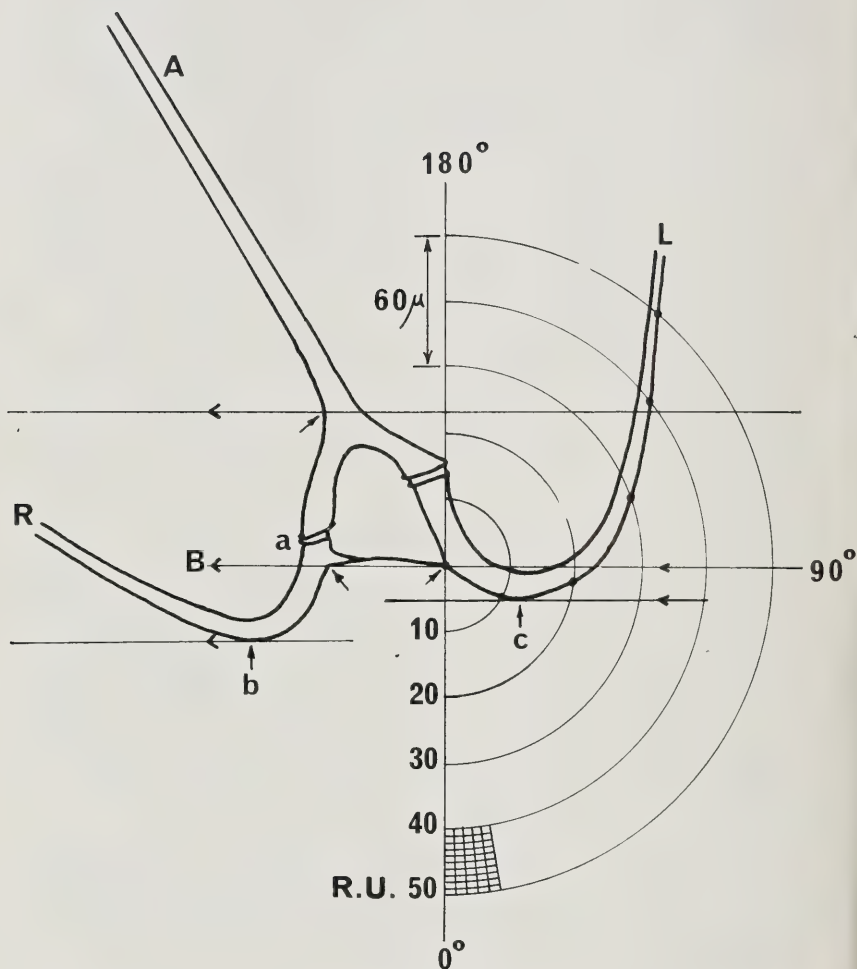


FIG. 2.

Showing how curvature of the left antapical horn is measured using polar coordinate graph paper. The arrows indicate the zero points for all three horns and the points of maximum backward curvature, (MBC), of the antapical horns. *A*, apical horn; *L* and *R*, left and right antapical horns; *B* posterior line; *a*, girdle; *b* and *c*, points of maximum backward curvature of antapical horns; *R.U.*, radius unit, one radius unit is approximately equal to 3μ.

specimens. Regressions were generally to the third degree, with about a third of the specimens showing a regression to the fourth degree. (See Appendix Table 1.)

These results are of no practical taxonomic use, chiefly because of the great variability in the curvature of the horns not encountered by Yarranton. The polar coordinates themselves, however, provide a satisfactory means of expressing horn curvature numerically.

TERMINOLOGY: The use of polar coordinates facilitates the construction of keys to, and taxonomic descriptions of, species of Section *Macroceras*, and the resultant terminology is given below:

Polar coordinates—degree and radius coordinates used here as a means of measuring the curvature of the antapical horns, plotted on camera lucida drawings of full ventral or dorsal aspect, at intervals of 15 μ , along the edges of the horns initially adjacent to the base of the hypotheca.

Radius unit—on the scale of the camera lucida drawings and the polar coordinate graph paper used, one radius unit is approximately equal to 3 μ . As this is only approximate, the radius coordinates are sometimes given in radius units or R.U.

Zero point for radius coordinates—the point of inception of the antapical horn immediately adjacent to the base of the hypotheca.

Posterior line—a line drawn to pass through the bases of the antapical horns at their inception immediately adjacent to the posterior margin of the hypotheca.

Zero line for degree coordinates—determined by drawing lines through the zero points of the right and left horns perpendicular to the posterior line.

MRC—the maximum rate of change of direction of curvature of a horn, measured in degrees over 15 μ after the initial curvature from 0–15 μ . (Very rarely, the MRC occurs over two, in exceptional cases three, successive 15 μ intervals.)

MBC—the point of maximum backward curvature of the horns determined by the construction of a tangent to the posterior or lower edge of the antapical horn parallel to the posterior line.

In addition, the ratios $\frac{B}{H}$ and $\frac{L90}{D}$ and $\frac{R90}{D}$, first defined by Jørgensen (1911), are of use in delimiting some of the taxa:

H is the perpendicular distance between a line joining the profile edges of the lower rim of the girdle and a line parallel to it through the left horn zero point for the radius coordinates.

B is the perpendicular distance between this latter line and a line parallel to it drawn as a tangent to the lower edge of the left antapical horn.

L90 and *R90* are the left and right horn radius coordinates with the 90° coordinate.

D is the diameter of the body measured in radius units.

The apical horn lies roughly perpendicular to the girdle in the specimens examined. Polar coordinates of this horn were measured along the left edge, with the base line a line drawn through the base of the horn parallel to the posterior line. The polar coordinates may indicate a very slight curvature of the apical horn, of insignificant use as a taxonomic character.

Subgenus *ORTHOCERATIUM* Sournia (1967): 376.

Gen. *Ceratium* Vanhöffen (1896): 133.

Sect. *Euceratium* Gran (1902): 192.

Subgen. *Euceratium* (Gran) Ostfeld (1903): 583.

Diagnosis: Differs from the other Subgenera in that, in normal vegetative cells, both antapical horns, very rarely only one, are either anteriorly directed from their inception, or at first posteriorly directed and then recurved forwards.

A key to the Sections will be given in a later paper.

Section *MACROCERAS* Ostfeld (1903): 584.

Sect. *Protuberantia* Karsten (1907): 404.

Subgen. *Macroceratium* Kofoid (1909): 218.

Böhm (1931b): 35.

Diagnosis: Distinguished by the curvature of the antapical horns, one or both of which are initially backwardly directed, usually markedly so; both antapical horns more or less similar in length.

KEY TO SUBSECTIONS

I Left antapical horn abruptly recurved before the 90° coordinate, so that it is posteriorly directed and lies roughly in line with the apical horn (See Fig. 7 H.)

Subsection *Reflexa*

II Left antapical horn never thus recurved.

(i) Chain formation rare, length of apical horn of posterior members of complete chain > 0,4 length of apical horn of front cell of chain.

Subsection *Macroceras*

(ii) Chain formation common, length of apical horn of posterior members of complete chain < 0,4 that of front cell of chain.

Subsection *Robusta*

HISTORY: Ostfeld (1903) distinguished between Section *Tripus* Ostf. and Section *Macroceras* on the grounds of closed distal ends to the antapical horns and spineless lists in the former, and antapicals with open distal ends and spiny lists in the latter. Karsten (1907) characterised Section *Protuberantia* as having the antapicals initially backwardly directed and then recurved anteriorly. He

divided this Section into Subsections: "*Ceratium tripos volans*, *C. tripos flagelliferum*, *macroceras*, *tergestina* and *robusta*", each of which corresponded to a single species, part of a species complex, or incorporated several species. Kofoid (1909) defined Subgenus *Macroceratium* as having antapical horns as in *Protuberantia* Karst., with the tips "truncate, open or contracted or rounded, but usually with a terminal pore". Jørgensen (1911) described Section *Macroceras* as having "both antapicals curved forward, open at the tip or rarely with closed ends, at least one antapical initially projecting more or less distinctly backwards . . . antapicals usually approximately the same length; this is however very variable within a single species; usually one to three more or less large wings at the base of the cell, which in Section *Tripos* are usually missing or very indistinct, with the exception of *C. compressum*, where they are similarly constructed." Jørgensen divided Section *Macroceras* into seven Subsections: "*Deflexa*, *Volantia*, *Vultur*, *Flagellifera*, *Tenuia*, *Intermedia* and *Reticulata*". This subdivision has not been followed by later authors, apart from Böhm (1931b), who divided "Subgenus *Macroceratium*" into Sections *Macroceras*, *Vultur*, *Trichoceros* and *Reticulata*. Section *Reticulata* (Jörg.) Böhm should be retained, in view of the peculiar hexagonal patterning of the thecal plates and the unusual alignment of the antapical horns.

Horn length and nature of ends of horns: Ostenfeld (1903) appears to have been the first author to comment on the nature of the ends of the antapical horns in this Section. Karsten (1905) in his description of "*C. tripos macroceras*" wrote: "sometimes the tips of the antapical horns are distinctly transversely truncate and open, without a piece appearing to be missing, in other cases they are certainly closed, which can be established especially when the ends are inflated . . . it is not unlikely that different stages of development are represented". In an illustration of a specimen of the *C. vultur* complex, "*C. tripos robustum*", Karsten (1907) shows the distal ends of the antapical horns fairly abruptly constricted and tapering to a tip terminating in a pore, (See Fig. 6T.) He also depicts antapical horn tips of specimens of Subsection *Macroceras* with rounded closed apices and slightly tapered open apices, (1907, Pl. 49). Pavillard (1907) wrote: "it is possible that the open ends, if constant in Section *Macroceras*, are the result of an early amputation, the mechanism of which is unknown." Kofoid (1908) came to the conclusion that the distal parts of the horns, in particular of the long-horned species, could be shed actively, a process he termed autotomy, and regenerate. He suggested that this was a flotation mechanism.

The nature of the ends of the antapical horns in Section *Macroceras* does not appear to have been discussed by later authors. The apical horn terminating in the apical pore, always has a truncate end, and usually it is not possible to determine whether or not the horn has been broken. In NGY specimens

belonging to this Section, the antapical horns were most frequently truncate, while in most specimens belonging to other Sections of the Subgenus *Orthoceratium*, the distal ends of the antapical horns tapered, with a decrease in wall thickness, to a closed point. Where the antapical horns were truncate, the wall of the horn was either of a uniform thickness, with an apparently open end, or the wall became gradually thinner distally, the horn tapering and ending in a rounded, rather than an abruptly truncate tip, which was occasionally slightly inflated. In the latter case, it was impossible to determine whether or not the end terminated in a pore. Cases of regeneration were observed, indicated by an abrupt transition between the thin-walled regenerated distal part and the thick-walled proximal part.

The foregoing indicates the difficulty in determining true horn length in specimens belong to this Section. Apical horn length along chains is, however, of importance in distinguishing between Subsections *Macroceras* and *Robusta*. (See Fig. 3.)

Subsection ROBUSTA Karsten (1907): 413.

Subsect. *Vultur* Jörgensen (1911): 71.

DIAGNOSIS: Differs from the other Subsections in that chain formation is common and the length of the apical horn in posterior members of the chain is less than 0,4 that of the anterior cell in a complete chain.

KEY TO SPECIES AND FORMS (Based upon polar coordinate measurements of antapical horn curvature. See Appendix Tables 2 and 3, and Fig. 4A-D.)

I Distal part of left antapical horn markedly recurved.

- (i) Zone of recurvature markedly angled and occurring between the 45 and 75 μ radius coordinates. *C. recurvum*

- (ii) Zone of recurvature gradual and occurring beyond the 120 μ radius coordinate. *C. vultur f. valdiviae*

II Distal part of left antapical horn not, or only very slightly recurved.

- (i) Left horn MBC radius coordinate $> 30 \mu$.

- (1) Left horn MRC $\geq 45^\circ$.

C. vultur f. japonicum

- (2) Left horn MRC $< 40^\circ$.

C. vultur f. vultur

- (ii) Left horn MBC radius coordinate $= 30 \mu$.

- (1) Left horn degree coordinate with 150 μ radius coordinate $> 150^\circ$.

C. vultur f. vultur

- (2) Left horn degree coordinate with 150 μ radius coordinate $< 150^\circ$.

C. vultur f. valdiviae

- (iii) Left horn MBC radius coordinate $< 30 \mu$.

- (1) Left horn MRC occurs between 60 and 90 μ radius coordinates.

C. vultur f. neglectum

- (2) Left horn MRC occurs before 45 μ radius coordinate.

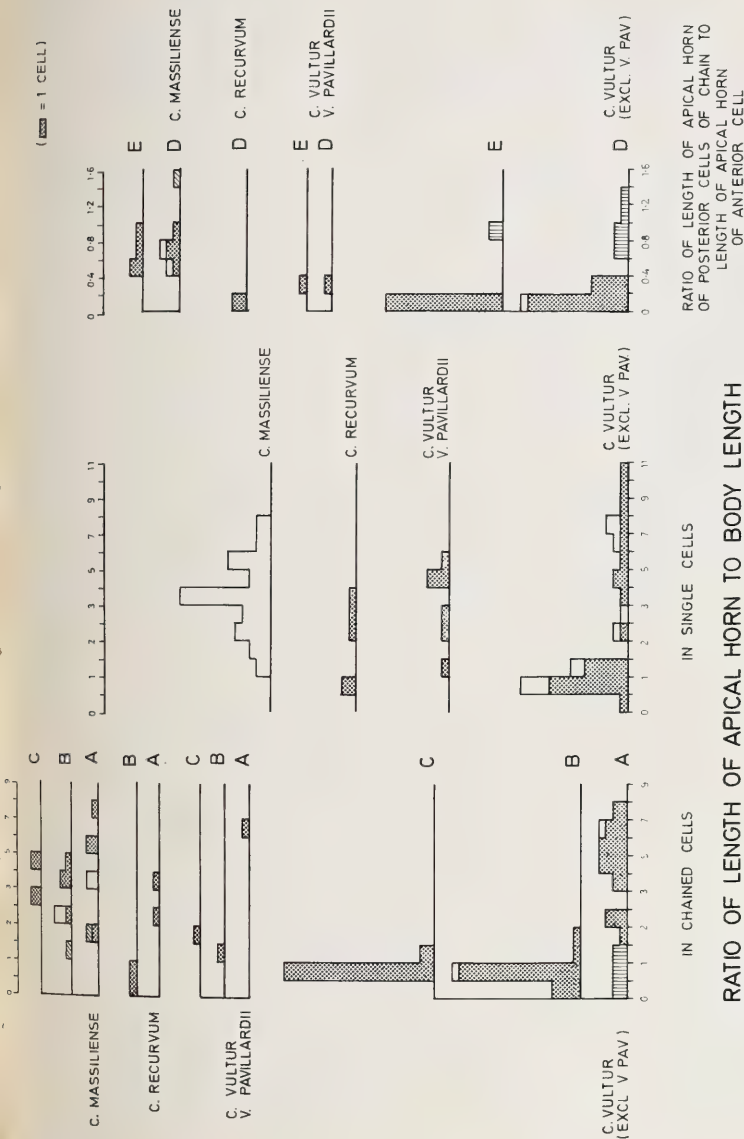
- (a) Left horn degree coordinate with 30 μ radius coordinate $\geq 100^\circ$.

- (b) Specimen from the Mediterranean.

C. vultur var. pavillardii

- (bb) Specimen from other waters.

C. vultur f. sumatranum



RATIO OF LENGTH OF APICAL HORN TO BODY LENGTH

FIG. 3.

Histograms showing variation in length of apical horn in Subsection *Robusta* Karst. compared with *C. massiliense* (Gourret) Karsten and a heteromorphic chain of *C. macroceros* (Ehbi.) Vanhoeffen, (in which the antapical horns of the anterior cell are short and straight). The white shading refers to specimens from Agulhas current NGY samples; the dotted to specimens from the literature; the vertical hatching to chains of *C. vultur* Cl. figured in the literature, in which the fragment of chain depicted lacked the long-apical-horned anterior cell; the diagonal hatching to the chain of *C. macroceros*. The only chains of Subsection *Macroceros* Jörg. depicted in the literature examined, (Kofoid (1908) fig. 10; Jörgensen (1911) Pl. I, fig. 6; Graham & Bronikowsky (1944) figs. 22 E, F; Wood (1954) fig. 235a), and all the figures of *C. vultur* cited in the text, are referred to. *A* refers to first cell of chain, *B* to second cell of chain, *C* to rest of cells of chain; *D* refers to ratio of length of apical horn of second cell of chain to that of first cell, *E* to ratio of length of apical horns of rest of cells of chain to that of first cell. (It is possible that the apical horn was broken in NGY specimens of *C. massiliense* with a low value for the ratio apical horn length: body length.)

- (aa) Left horn degree coordinate with $30\ \mu$ radius coordinate $< 100^\circ$.
- (c) Right horn MBC radius coordinate $> 22\ \mu$, left horn degree coordinate with $90\ \mu$ radius coordinate $< 145^\circ$.
- (cc) Right horn MBC radius coordinate $< 22\ \mu$, left horn degree coordinate with $90\ \mu$ radius coordinate $> 145^\circ$.

C. vultur f. valdiviae

C. vultur f. sumatranum

Members of Subsection *Robusta* are not common in phytoplankton samples, and extensive use had to be made of figures from the literature to obtain a good picture of taxonomic variation. Unfortunately these figures are not always accurate (such as Schröder's (1900) illustration of a chain of "*C. tripos* var. *macroceras f. undulata*", see Fig. 5A).

The retention of this Subsection is justified by the difference between the apical horn length of the front cell of a complete chain and that of the rest of the cells. In 63% of the cells belonging to this Subsection figured in the literature and found in the Agulhas current NGY samples, the apical horn was < 1.5 the body length, while this was the case in only 4.5% of the NGY cells of *C. massiliense* (Gourret) Karst., where it is possible that the apical horn was broken. (See Fig. 3.)

Culture experiments on members of this Subsection are needed to determine whether or not the daughter cells always adhere together forming chains for at least some time after schizogony; whether the posterior daughter cell of a division always has a short apical horn; whether a short-apical-horned cell could, on division produce a long-apical-horned cell; and whether a short apical horn could later increase in length.

Ceratium vultur Cleve (1900): 15, Pl. 7, fig. 5. (See Figs. 4-9.)

Description: An extremely variable species, forming chains, in which the length of the apical horn of the posterior cells is < 1.5 the body length and < 0.4 the length of the apical horn of the front cell. The posterior cells of a chain may also differ from the anterior cell, and sometimes from one another in the curvature of the antapical horns, the MBC degree and radius coordinates, the ornamentation of the theca, body shape and girdle diameter. *Antapical horn curvature:* The antapical horns may lie parallel to one another and the apical horn, or diverge; sometimes, usually in posterior chain cells, the distal parts are smoothly recurved. Measured values of the left horn degree coordinate with the $15\ \mu$ radius coordinate vary from $28-105^\circ$, usually $50-85^\circ$, while the equivalent right horn degree coordinate is less or greater than its left counterpart by up to 38° . The left horn MBC degree coordinate varies from $40-90^\circ$, mostly $60-80^\circ$, and the MBC radius coordinate from $6-72\ \mu$; the right horn MBC degree coordinate is from 33° less to 24° greater than that of the left horn, and the right horn MBC radius coordinate varies from $6-45\ \mu$, very rarely $60\ \mu$.

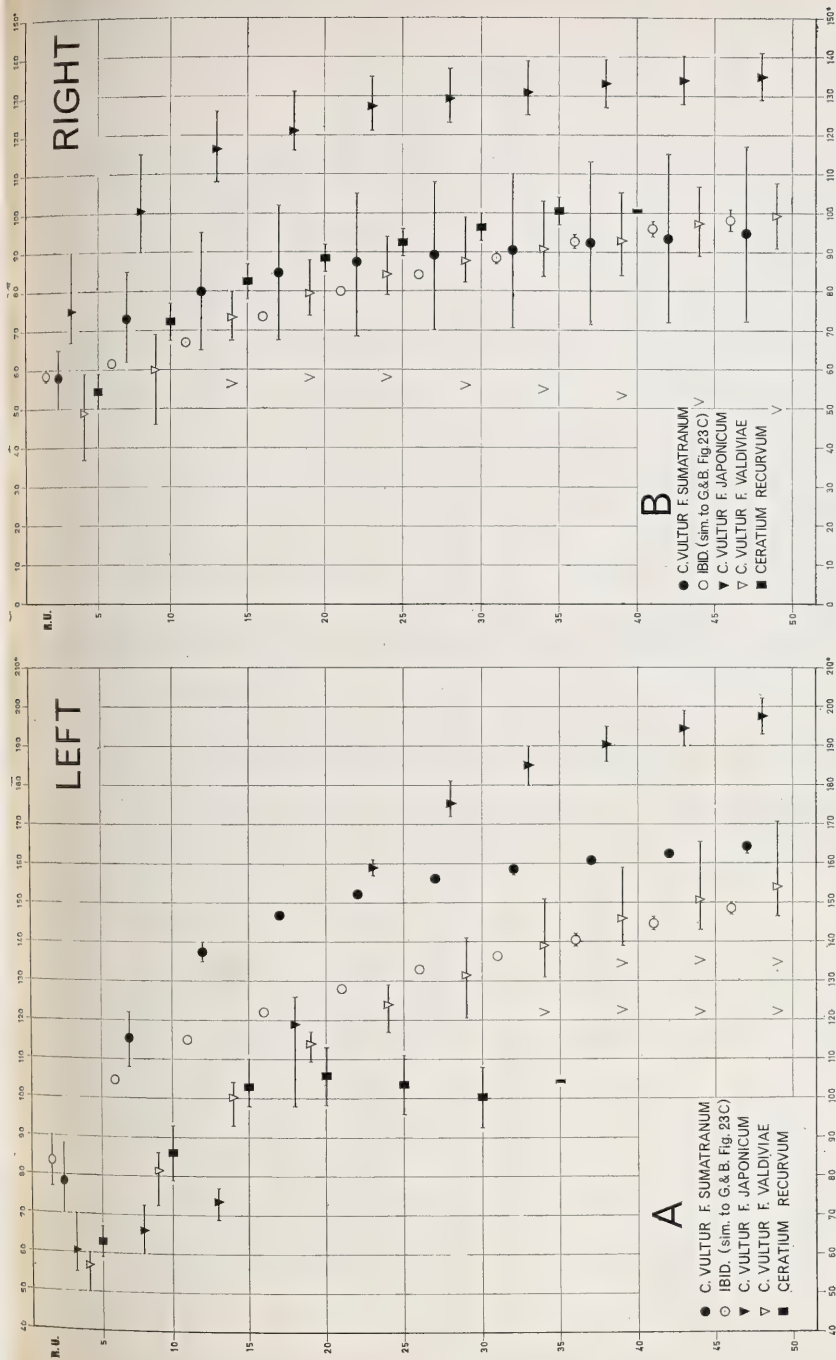


FIG. 4. (a & b)

Antapical horn curvature in NGY specimens of *C. vultur* and *C. recurvum* (Jörg.) Reinecke: *A*, curvature of the left horn expressed in polar coordinates, that is in degrees at intervals of 5 R.U. from 5 to 50 R.U.; (R.U. = radius unit, one radius unit is approximately equal to 3μ); the symbols represent the mean degree coordinate values at successive 5 R.U. intervals for all specimens examined, the lines indicate the range of degree values recorded; *B*, the same for the right horn; half symbols represent single specimens.

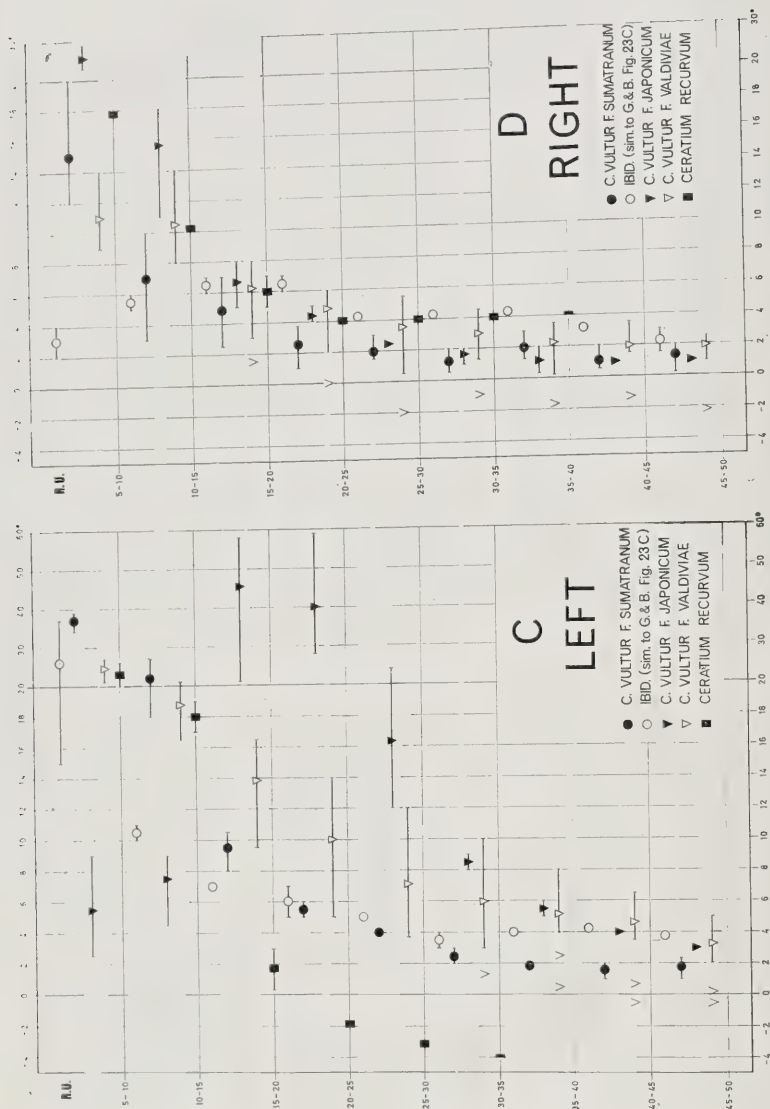


FIG. 4. (c & d)

C, rate of change of direction of curvature of left horn, expressed in degrees over 5 R.U., from 5-10 to 45-50 R.U.; D, the same for the right horn; half symbols represent single specimens.

In forms with a large left horn MBC radius coordinate, the equivalent right horn coordinate is considerably smaller. *Body shape*: This varies with regard to the length-breadth ratio, the relative length of the epi- and hypo- thecae and the angle made by a projection of the girdle and the base of the hypotheca. (See Fig. 9.) *Thecal ornamentation*: Seen in full ventral aspect, lists, other than the usual sulcal list, may occur along the proximal part or almost the entire length, of the right and left sides of the apical horn, extending on to the epitheca; along the base of the hypotheca, extending onto the proximal parts, sometimes continuing for almost the entire length, of the antapical horns, and along the proximal parts or almost the entire length of their upper sutures. The margins of the lists may be smooth, serrate or denticulate; sometimes spines or denticles occur along the base of the list, not extending across it; sometimes along the apical horn and in the region of recurvature on the lower side of the left horn, (very rarely the right), one to a number of spines traverse the list as supporting spines. The degree of listing varies from the above-mentioned to complete absence. Spines and/or denticles may occur along the horns in the absence of lists, when the spines may be slightly longer along the apical horn and region of recurvature of the lower suture of the left horn, or there may be combinations such as: lists along the apical horn and spines along the lower margins of the antapicals, etc. The thecal wall varies from being thin to heavily thickened and ridged.

Distribution: *C. vultur* is a fairly rare warm water species. Graham & Bronikowsky (1944) classify it as an intolerant shade species, that is, closely restricted to waters with surface temperatures of 19°C or higher, and increasing in frequency from 0–100 m. *C. vultur* var. *pavillardii* is the only infraspecific category to be recorded from the Mediterranean. The other forms are recorded from all oceans, but only *f. japonicum*, *f. valdiviae* and *f. sumatranum* were found in the NGY samples. (See Table 1.)

This is the most variable species in the genus, and the treatment of the many infraspecific categories is a difficult problem. The various taxa recorded have been described from single cells, or short chains of similar individuals, and some of these taxa have later been found in chains with other taxa, or chains with intermediate characters have been discovered. Culture experiments, difficult to carry out because of the paucity of *C. vultur* in plankton samples, are very necessary to determine the nature of variation in this species.

Peters (1932) was the first author to consider the components of *C. vultur*, excluding var. *pavillardii*, as belonging to a single species, in which infraspecific categories were not justified. Steemann Nielsen (1934) treated these, excluding var. *pavillardii*, as varieties, but later (1939), he noted: "Beim Indischen Material war es immer möglich, *C. vultur* und *C. sumatranum* auseinanderzuhalten."

NGY Stations	MARCH						MAY					
	11*	12	13	14	15	16	41*	42	43	44	45	46
Surface temperature	20.66	24.28	25.49	23.78	22.19	21.62	17.49	23.27	24.15	23.50	21.25	20.90
Temperature at 100 m	13.26 (at 50 m)	17.53	19.65	19.52	18.73	18.61	16.66 (at 50 m)	12.21	19.99	20.54	20.50	20.37
No. slides examined	4	4	4	4	4	8	4	5	7	4	4	5
Total number ceratia	601	191	233	267	270	241	1 803	318	92	184	241	365
C. VULTUR F. SUMATRANUM	—	0.52%	0.42%	—	0.37%	—	0.16%	—	4.34%	1.01%	0.41%	—
C. VULTUR F. VALDIVIAE	—	2.09%	1.28%	—	—	—	0.38%	—	—	—	—	—
C. VULTUR F. JAPONICUM	—	—	0.42%	0.37%	—	—	0.11%	—	1.08%	—	—	—
CERATIUM RECURVUM	—	—	0.85%	—	—	—	0.11%	—	—	—	—	—
CERATIUM REFLEXUM	—	—	—	—	—	—	0.00%	—	—	—	0.41%	—
												0.07%

TABLE 1.

Showing distribution and relative frequency, expressed as a percentage, of species of Subsections *Robusta* and *Reflexa* in samples from the line of NGY stations off Port Elizabeth. Apart from the * stations, net hauls examined from 100-0 m. (Temperatures in °C.)

He found their distribution and ecology identical. Graham and Bronikowsky (1944) concluded that seven varieties of *C. vultur*, including *var. pavillardii*, could be distinguished, but gave no measurements and no figures of chains.

An examination of specimens illustrated in the literature indicates no sharp visual discontinuities between the various taxa described. (See Figs. 5 and 6.) Polar coordinates of some of these were measured on enlargements similar in scale to the camera lucida drawings of the NGY specimens. While no absolute discontinuities are apparent, it is possible to construct a key using polar coordinates to all the variations depicted, bearing in mind the inaccuracies of some of the figures (see Appendix Table 2). The NGY specimens alone are easily classified into disjunct groups (see Appendix Table 3).

It is felt that a retention of infraspecific categories in this species is necessary, as the typical representatives are easily recognisable in the absence of intermediates. The use of infraspecific epithets in describing specimens of *C. vultur* in lists of phytoplankton flora serves as a brief indication of the variation of the species in the particular area under study.

The lowest botanical taxonomic ranks are those of *forma* and the rarely used *subforma*, and the concept of these varies from species to species, depending upon the nature of infraspecific variation. Here, with one exception, the rank of *forma* is applied to all reasonably disjunct taxa of *C. vultur*, bearing in mind that two forms may occur in the same chain.

Ceratium vultur f. vultur

"*C. (tripos var. ?) vultur* N.Sp." Cleve (1900): 15, Pl. 7^c fig. 5.

Okamura & Nishikawa (1904): 123, Pl. 6, Fig. 8.

C. vultur: Jörgensen (1911): 71, Pl. 8, Fig. 151a*, p.p. (posterior cell), 151b; Dangeard (1927): 378, Fig. 42b*, p.p. (posterior cell); Pavillard (1931): 93, Pl. 3, Fig. 8*; Peters (1932): 54, Pl. 1, Fig. 7b; Steemann Nielsen (1934): 27, Fig. 65; Schiller (1937): 418, Fig. 459a* (from Jörgensen (1911) Fig. 151a).

C. japonicum: Pavillard (1931): 93, Pl. 3, Fig. 9*, p.p. (posterior cell); Balech (1962): 182, Pl. 25, Fig. 393*, p.p. (posterior cell).

C. vultur f. japonicum: Wood (1954): 304, Fig. 233c*, p.p. (posterior cell).

C. pavillardii: Wood (1954): 304, Fig. 232a; *non C. pavillardii* Jörgensen.

C. tripos robustum: Karsten (1907): 413, Pl. 48, Fig. 13a*, p.p. (posterior cell), 13b.

(Intermediate between *f. vultur* and *f. valdiviae*: Jörgensen (1911) Fig. 151a, anterior cell.)

Diagnosis: Differs from *f. japonicum* with which it is sometimes associated in the same chain as the posterior member(s), in that, in the left horn the MRC is

*Chain depicted.

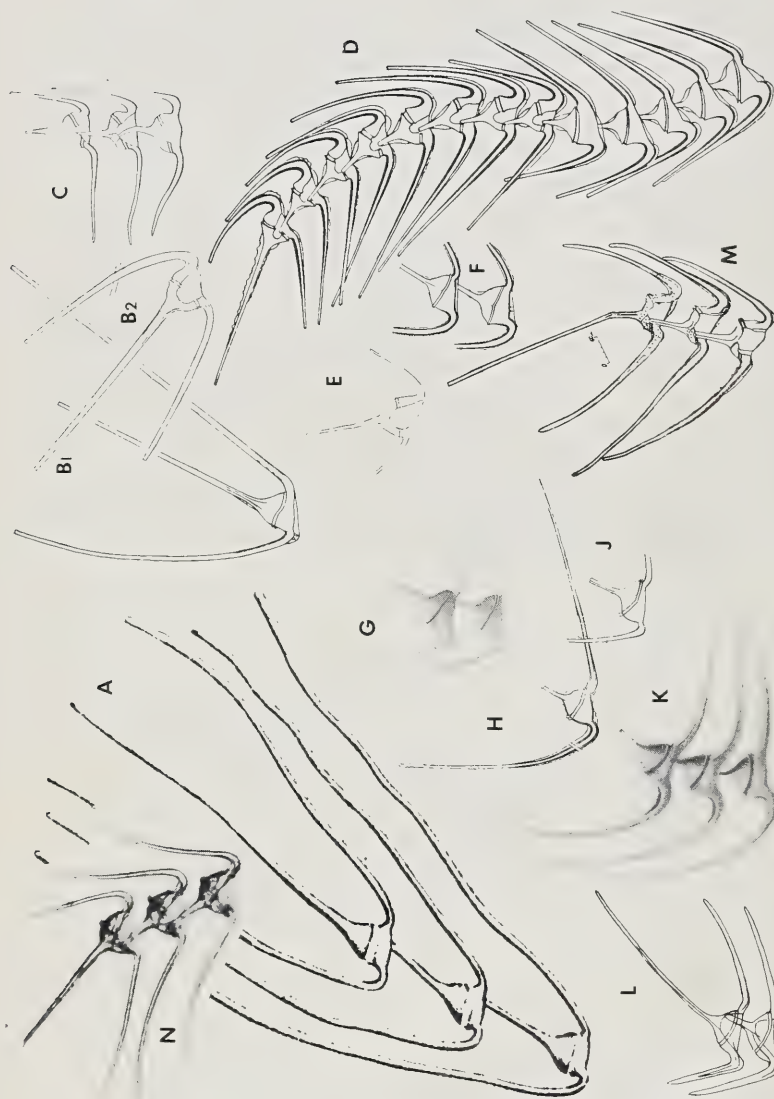


Fig. 5.

A selection of specimens of *C. vultur* depicted in the literature: A, Schröder (1900) Pl. 1, fig. 17m, "*C. tripos* var. *macroceras* f. *undulata*" = var. *pavillardii*; B1 Pavillard (1905) Pl. 1, fig. 2, "*C. vultur*" = var. *pavillardii*; B2 Rampi (1939) fig. 41, "*C. pavillardii*" = var. *pavillardii*; C Ballantyne (1961) fig. 55, "*C. vultur* var. *sumatranum*" = f. *sumatranum*; D Kofoid (1909) Pl. 4, fig. 7, "*C. vultur*" = f. *sumatranum*; E Böhm (1931a) fig. 19, "*C. pavillardii*" short horned winter form = var. *pavillardii*; F Kofoid (1908) fig. 9, "*C. vultur*" = f. *sumatranum*; G Karsten (1907) Pl. 51, fig. 14, "*C. tripos* vultur var. *sumatrana*" = f. *sumatranum* (iconotype); H Jörgensen (1911) Pl. 8, fig. 154, "*C. sumatranum*" = f. *valdiviae*; I Ibid. fig. 135, "*C. sumatranum* f. *angulatum*" = f. *sumatranum*; J Karsten (1905) Pl. 19, fig. 12a, "*C. tripos* f. *neglecta*" = f. *valdiviae*; L Ostenfeld & Schmidt (1901) fig. 20, "*C. vultur*" = f. *sumatranum*; M Nie (1936) fig. 32, "*C. sumatranum*" = f. *sumatranum*; N Klement (1964) "*C. vultur*" = f. *sumatranum*.

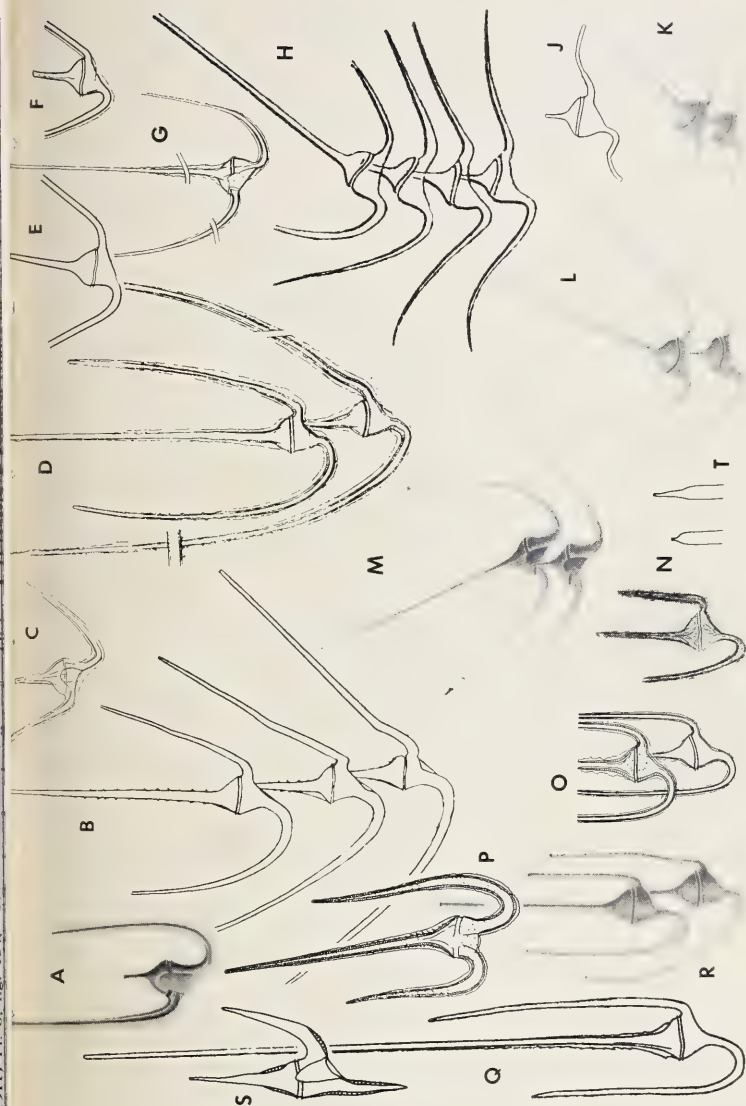


FIG. 6.

A selection of specimens of Subsections *Robusta* and *Reflexa* depicted in the literature: A Karsten (1905) Pl. 19, fig. 12, "*C. tripos f. neglecta*" = *C. vultur f. neglectum* (iconotype); B Pavillard (1931) Pl. 3, fig. 8, "*C. vultur*" = *C. vultur f. vultur* (iconotype); C Cleve (1900) Pl. 7, fig. 5, "*C. vultur*" = *C. vultur f. vultur* (iconotype); D Jørgensen (1911) Pl. 8, fig. 151a, "*C. vultur*", post. cell = *C. vultur f. vultur*, ant. cell = intermediate between *f. vultur* and *f. valdiviae*; E Graham & Bronikowsky (1944) fig. 23G, "*C. vultur var. regularis*" = *C. massiliense*; F Ibid. fig. 23B, "*C. vultur var. reversum*" = *C. vultur f. sumatranum*; G Jørgensen (1911) Pl. 8, fig. 153, "*C. sumatranum*" = *C. vultur f. valdiviae*; H Okamura (1907) Pl. 3, fig. 1a, "*C. vultur*" = *C. vultur f. valdiviae*; I Steemann Nielsen (1934) fig. 66, Pl. 48, figs. 14a, b, "*C. tripos vultur*" = *C. recurvum*; K Karsten (1907) Pl. 52, fig. 8, "*C. tripos buccerosus*" = *C. recurvum*; L M Karsten (1907) Pl. 48, figs. 14a, b, "*C. tripos vultur*" = *C. vultur f. valdiviae*; N Osenfeld & Schmidt (1901) fig. 17, "*C. robustum*" = *C. vultur f. japonicum*; O Böhm (1931b) fig. 35b, "*C. vultur*", ant. cell = *C. vultur f. neglectum*, post. cell = *f. japonicum*; P Schröder (1906) fig. 31, "*C. robustum forma*" = *C. vultur f. japonicum*, ant. cell = *C. vultur f. japonicum*, post. cell = *C. vultur f. japonicum* (iconotype); Q Schröder (1906) fig. 33c, "*C. japonicum*" = *C. vultur f. japonicum*, post. cell = *C. vultur f. japonicum*; R Karsten (1907) Pl. 48, fig. 13a, "*C. tripos robustum*", ant. cell = *C. vultur f. vultur*; S Wood (1963b) fig. 53, "*C. vultur var. productum*" = *C. reflexum*; T Karsten (1907) Pl. 48, fig. 13c, "*C. tripos robustum*", ends of antapical horns.

$< 40^\circ$ and the degree coordinate with the $150\ \mu$ radius coordinate is $< 170^\circ$; differs from *f. neglectum* in that in the left horn the MBC radius coordinate is $\geq 30\ \mu$ and the coordinate with the $150\ \mu$ radius coordinate is $< 170^\circ$; differs from *f. valdiviae* in that in the left horn the MBC radius coordinate is generally $> 30\ \mu$ and the coordinate with the $150\ \mu$ radius coordinate is $> 150^\circ$; differs from *f. sumatranum* in that the left horn MBC radius coordinate is $\geq 30\ \mu$. (See Fig. 6B–D, R.)

Dimensions: From literature: Jörgensen (1911), girdle diameter $57\text{--}62\ \mu$; length left profile of hypotheca from base of horn to lower girdle list $36\text{--}38\ \mu$; length long apical horn $300\ \mu$ or more; length short apical horn $85\text{--}100\ \mu$.

The cell depicted by Cleve is a short-apical-horned posterior cell. Both monomorphic chains, with the long-apical-horned anterior cell similar to Cleve's iconotype (eg. Pavillard (1931) Pl. 3, Fig. 8), and dimorphic chains with the anterior cell belonging to *f. japonicum*, (eg. Karsten 1907), have been recorded. The long-apical-horned anterior cell of the chain figured by Jörgensen (1911, Fig. 151a), has a short left horn MBC radius coordinate, and differs from the anterior cell of a chain of *f. valdiviae* depicted by Karsten (1907, Pl. 48, Fig. 14b), only in the shorter MBC radius coordinate of the right horn.

Ceratium vultur f. japonicum (Schröder) Wood (1954): 305, Fig. 233c*, p.p. (anterior cell).

Sournia (1967): 481, Fig. 96.

C. japonicum Schröder (1906): 361, Fig. 33 a–c; Pavillard (1931): 93, Pl. 3, Fig. 9*, p.p. (anterior cell); Balech (1962): 182, Pl. 25, Fig. 393*, p.p. (anterior cell).

C. vultur var. *japonicum* (Schr.) Jörgensen (1911): 73, Pl. 8, Fig. 152a, b; Graham & Bronikowsky (1944): 41 Fig. 23E.

C. vultur: Dangeard (1927): 378, Fig. 42b*, p.p. (anterior cell); Böhm (1931b): 38, Fig. 35b*, p.p. (posterior cell); Peters (1932): 54, Pl. 1, Fig. 7b; Schiller (1937): 418, Fig. 459b (from Jörgensen (1911) Fig. 152).

C. robustum Ostenfeld & Schmidt (1901): 166, Fig. 17; Schröder (1906): 361, Fig. 31.

C. tripos robustum (O. & S.) Karsten (1907): 413, Pl. 48, Fig. 13a*, p.p. (anterior cell).

C. pavillardii: Wood (1954): 304, Fig. 232b.

Diagnosis: Differs from *f. vultur*, with which it is sometimes associated in chains as the anterior long-apical-horned cell, in that the recurved part of the antapical horns and the apical horn all lie parallel to one another, the left horn

*Chain depicted

degree coordinate with the 150 μ radius coordinate being $\leq 175^\circ$, (except in specimens with a very long left horn MBC radius coordinate, when it is less), and the left horn MRC is $\geq 45^\circ$; differs from *f. neglectum*, with which it has been recorded in a chain as the posterior cell and also *f. valdiviae* and *f. sumatranum* in that the left horn MBC radius coordinate is $>30 \mu$; differs further from *f. valdiviae* in that the left horn MRC is $>40^\circ$. (See Figs. 6N–R and 7D, E.)

Dimensions: In specimens examined: Girdle diameter 54–66 μ ; length hypotheca 30–39 μ ; length epitheca from centre of top girdle list to base of apical horn, 15–24 μ ; length long apical horn 480–570 μ . *From literature:* Girdle diameter 54 μ ; length hypotheca 38 μ ; length long apical horn 770 μ .

All chains incorporating *f. japonicum* depicted in the literature are dimorphic and two celled, with the posterior cell *f. vultur*, or the anterior cell *f. neglectum*. In NGY samples, only single, long-apical-horned cells were recorded.

Ceratum vultur f. neglectum (Karsten) Reinecke comb. nov.

C. tripos f. neglecta Karsten p.p. (1905): 146, Pl. 19, Fig. 12 non 12a.

C. vultur: Böhm (1931b): 38, Fig. 35b*, p.p. (anterior cell); Wood (1954): 304, Fig. 233a.

C. vultur var. japonicum: Graham & Bronikowsky (1944): 41, Fig. 23F.

Diagnosis: Differs from *f. japonicum* with which it has been recorded as the anterior long-apical-horned cell in a chain, in that the left horn MBC radius coordinate is $<30 \mu$; differs from *f. vultur* in that in the left horn the MBC radius coordinate is $<30 \mu$, the degree coordinate with the 150 μ radius coordinate is $>170^\circ$ and the recurved parts of the antapical horns lie roughly parallel to the apical horn; differs from *f. valdiviae* and *f. sumatranum* in that the left horn MRC occurs beyond the 45 μ radius coordinate. (See Fig. 6A, O.)

The single cells depicted in the literature have short apical horns. The specimen figured by Graham and Bronikowsky (1. c.) is unusual in that the angle made by a projection of the girdle and the hypothecal base is very large for the species, being 58° .

Ceratum vultur f. valdiviae Reinecke forma nova.

C. vultur: Okamura (1907): 129, Pl. 3, Figs. 1a*, 1c*.

C. vultur var. vultur: Graham & Bronikowsky (1944): 41, Fig. 23H.

C. tripos vultur: Karsten (1907): 414, Pl. 48, Figs. 14a*, b*.

C. sumatranum: Jörgensen p.p. (1911): 73, Pl. 8, Figs. 153, 154; Dangeard (1927):

*Chain depicted

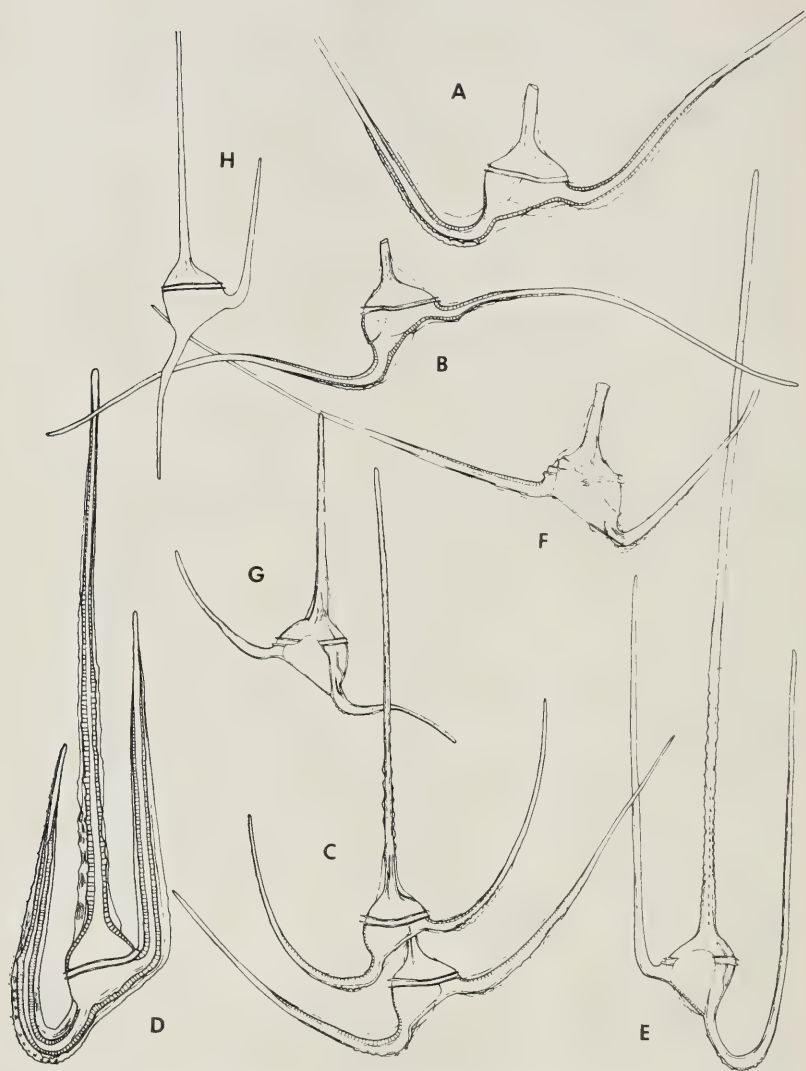


FIG. 7.

Specimens of Subsections *Robusta* and *Reflexa* from NGY Agulhas current samples: A—C *C. vultur* f. *valdiviae* Reinecke f. nov.; D and E *C. vultur* f. *japonicum* (Schröder) Wood; F *C. vultur* f. *sumatranum* (Karsten) Sournia; G *C. recurvum* (Jörgensen) Reinecke; H *C. reflexum* Cleve. Girdle diameters: A 63 μ , B 57 μ , C 54 μ , D 66 μ , E 54 μ , F 60 μ , G 57 μ , H 54 μ .

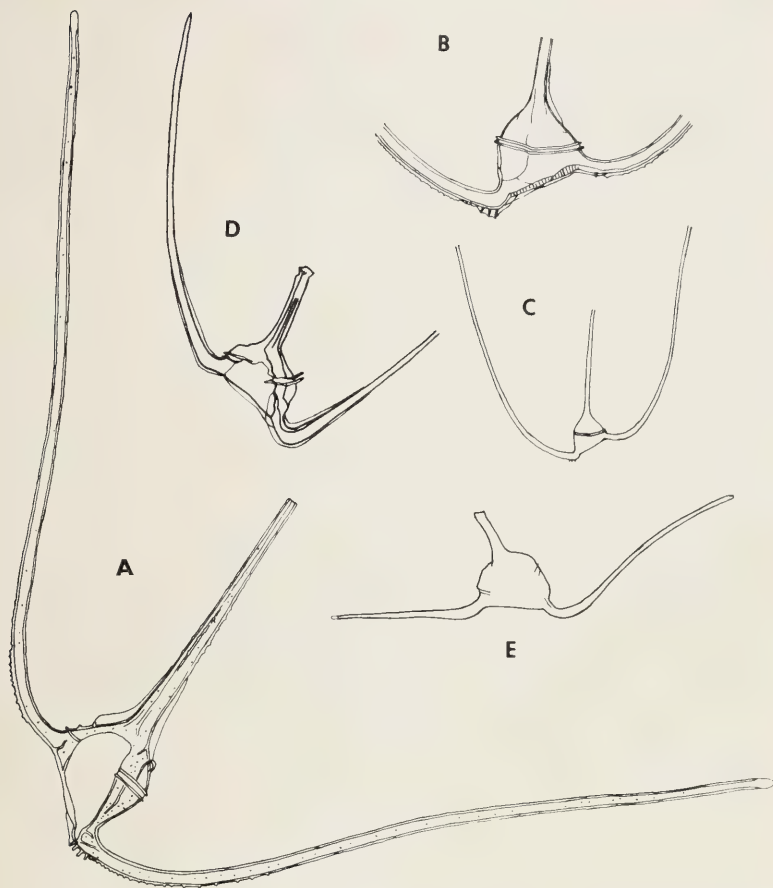


FIG. 8.

Specimens of *C. vultur* Cleve from NGY Agulhas current samples: A—D *C. vultur* f. *sumatranum* (Karsten) Sournia, B is an enlargement of the body and horn bases of C; E *C. vultur* f. *valdiviae* Reinecke f. nov. Girdle diameters: A 72 μ , B 66 μ , D 60 μ , E 54 μ .

378, Fig. 42c*; Böhm (1931b): 38, Fig. 35c*, Pl. 1; Balech (1962): 182, Pl. 25, Fig. 394*.

C. vultur var. *sumatranum*: Steemann Nielsen p.p. (1934): 27; Schiller (1937): 419, Fig. 460a, b (from Jörgensen (1911) Figs. 153, 154); Graham & Bronikowsky (1944): 41, Fig. 23D.

*Chain depicted

C. tripos neglectum Karsten p.p. (1905): 146, Pl. 19, Fig. 12a*, non Fig. 12.

Diagnosis: Differt a speciminibus multis *f. sumatrani* in eo quod °coordinatus cornus sinistri cum coordinato radii $30\ \mu < 100^\circ$ est; differt ab illis speciminibus *f. sumatrani* in quibus hic coordinatus $< 100^\circ$ est in eo quod °coordinatus cornus sinistri cum coordinato radii $90\ \mu < 145^\circ$ est, et coordinatus radii cornus dextri in loco flexi maximi retrorsum $> 22\ \mu$ est; differt a *f. vulture* in eo quod coordinatus radii cornus sinistri in loco flexi maximi retrorsum plerumque $< 30\ \mu$ est; specimina in quibus hic coordinatus $30\ \mu$ aequans a speciminibus rarissimis *f. vulturis* in quibus hic coordinatus $30\ \mu$ aequans differunt in eo quod °coordinatus cornus sinistri cum coordinatus radii $150\ \mu < 150^\circ$ est; differt a *f. neglecto* in eo quod in cornu sinistro, cursus mutationis maximi flexus per $15\ \mu$ intra coordinatum radii $45\ \mu$ accidit et °coordinatus cum coordinatus radii $150\ \mu < 170^\circ$ est; differt a *f. japonico* in eo quod cursus mutationis maximi flexum per $15\ \mu < 40^\circ$ est.

Diagnosis: Differs from most specimens of *f. sumatranum* in that the left horn degree coordinate with the $30\ \mu$ radius coordinate is $< 100^\circ$, and from those specimens of *f. sumatranum* in which this coordinate is $< 100^\circ$ in that the left horn degree coordinate with the $90\ \mu$ radius coordinate is $< 145^\circ$ and the right horn radius coordinate at the point of maximum backward curvature is $> 22\ \mu$; differs from *f. vultur* in that the left horn radius coordinate at the point of maximum backward curvature is generally $< 30\ \mu$, specimens in which this coordinate equals $30\ \mu$ differ from the occasional specimens of *f. vultur* in which this coordinate is $30\ \mu$ in that the left horn degree coordinate with the $150\ \mu$ radius coordinate is $< 150^\circ$; differs from *f. neglectum* in that in the left horn the maximum rate of change of direction of curvature over $15\ \mu$ occurs before the $45\ \mu$ radius coordinate and the degree coordinate with the $150\ \mu$ radius coordinate is $< 170^\circ$; differs from *f. japonicum* in that the left horn MRC is $< 40^\circ$. (See Figs. 5K, 6G, H, L, M, 7A–C and 8E.)

Dimensions: In specimens examined: Girdle diameter $54\text{--}63\ \mu$; length hypotheca $24\text{--}42\ \mu$; length epitheca $18\text{--}24\ \mu$; length long apical horn $348\ \mu$; length short apical horn $30\text{--}54\ \mu$. From literature: Jörgensen (1911), including *f. sumatranum*, diameter $64\text{--}71\ \mu$; length hypotheca $40\text{--}43\ \mu$; length apical horn $30\text{--}110\ \mu$, sometimes up to $400\ \mu$.

In chains with a long-apical-horned anterior cell, the antapical horns of the front cell are more forwardly directed than in the posterior cells. Recurvature of the distal parts of the antapical horns, usually only in the posterior cells, is quite common.

In NGY specimens, *f. valdiviae* was easily distinguished from *f. sumatranum*, but a survey of the literature indicates that the differences between the two are not sharp. Intermediates between *f. valdiviae* and *f. vultur* occur, but the former has never been recorded in chains with *f. japonicum*.

It is of interest to note that both *f. valdiviae* and *f. neglectum* were originally recorded by Karsten (1905) in only one and the same Atlantic sample.

Ceratiium vultur f. sumatranum (Karsten) Sournia (1967) p.p.: 482.

C. tripos vultur var. sumatrana Karsten (1907): 413, 414, Pl. 48, Fig. 15a, b, Pl. 52, Fig. 14*.

C. vultur var. sumatranum (Karst.) Steemann Nielsen (1934) p.p.: 27, non Fig. 66; Schiller (1937) p.p.: 419, non Fig. 460; Wood (1954): 305, Fig. 233d; Ballantine (1961): 255, Fig. 55*.

C. sumatranum (Karst.) Jörgensen (1911) p.p.: 73, non Pl. 8, Figs. 153, 154; Nie (1936): 68, Figs. 31, 32*.

C. sumatranum f. angulatum Jörgensen (1911): 74, Pl. 8, Fig. 155.

C. vultur: Ostenfeld & Schmidt (1901): 167, Fig. 20*; Okamura (1907): 129, Pl. 3, Fig. 1b; Kofoed (1908) Fig. 9*; Kofoed (1909) Pl. 4, Fig. 7*; Klement (1964): 356, Pl. 2, Fig. 4*.

C. vultur var. reversum Graham & Bronikowsky (1944): 41, Fig. 23B.

C. vultur var. pavillardii: Graham & Bronikowsky (1944) p.p.: 41, Fig. 23C; non *C. pavillardii* Jörgensen.

Diagnosis: Generally differs from all other forms in that the left horn degree coordinate with the 30 μ radius coordinate is $\geq 100^\circ$, specimens of *f. sumatranum* in which this coordinate is $< 100^\circ$ differ from *f. valdiviae* in that the left horn degree coordinate with the 90 μ radius coordinate is $> 145^\circ$ and the right horn MBC radius coordinate is $< 22 \mu$; differs from *f. vultur* and *f. japonicum* in that the left horn MBC radius coordinate is $< 30 \mu$; differs from *f. neglectum* in that the left horn MRC occurs before the 45 μ radius coordinate. *f. sumatranum* is distinguished from *var. pavillardii* solely on grounds of distribution: the latter is confined to the Mediterranean, and is the only infraspecific taxon of *C. vultur* occurring there. (See Figs. 5C, D, F, G, J, L-N, 6F, 7F and 8A-D.)

Dimensions: *In specimens examined:* Girdle diameter 60–72 μ ; length hypotheca 27–42 μ ; length epitheca 15–36 μ ; length short apical horn 57–66 μ ; length long apical horn 210 μ . *From literature:* girdle diameter 43–71 μ ; length hypotheca 23–43 μ ; length short apical horn 34–110 μ ; length long apical horn up to 400 μ .

Karsten (1907: 413) referred to his new variety and the curvature of its antapical horns thus: “. . . hier finden sich ein Novum darin das es zu direkt Knickungen kommt, oder doch zu Krümmungen von so geringem Radius das der Eindruck von Knickungen hervorgerufen werden muss. Im Atlantischen Ocean scheinen die Formen zu fehlen . . .” It was Jörgensen (1911), who expanded the concept of “*C. sumatranum*” to include specimens of *f. valdiviae*.

*Chain depicted

Karsten himself (1907: 414), considered his "*C. tripos* var. *neglecta*" of 1905 to be characteristic of "*C. tripos* *vultur*".

F. sumatranum has been recorded singly and in complete monomorphic chains.

Ceratium vultur* var. *pavillardii (Jørgensen) Graham & Bronikowsky (1944) p.p.: 41, *non* Fig. 23C.

C. pavillardii Jørgensen (1911): 74, Pl. 9, Fig. 157a, b; (1920): 92, Fig. 83; Forti (1921): 70, Pl. 5, Fig. 56; Paulsen (1930): 90; Böhm (1931a): 364, Fig. 19; Rampi (1939): 307, Fig. 41; Halim (1960) Pl. 5, Fig. 8; *non* Dangeard (1927): 378 Fig. 42a (= *C. massiliense* (Gourret) Karst.); *nec* Wood (1954): 304, Fig. 232a, b (= *f. vultur*, *f. japonicum*).

C. vultur: Pavillard (1905): 54, Pl. 1, Fig. 2.

C. tripos var. *macroceras* *f. undulata* Schröder (1900): 16, Pl. 1, Fig. 17m*.

Diagnosis: Differs from *f. sumatranum* in that it occurs only in the Mediterranean, from which *f. sumatranum* is absent; differs from the other forms in that the left horn degree coordinate with the 30 μ radius coordinate is $> 100^\circ$.

Description: *Antapical horn curvature* similar to that in *f. sumatranum*: left horn degree coordinate with 30 μ radius coordinate $> 100^\circ$; left horn MBC radius coordinate $\leq 15 \mu$, this horn sometimes directed forwards from inception; MRC of right horn occurs between the 15 and 30 μ radius co-ordinates, rarely between the 30 and 45 μ , or between the 45 and 60 μ radius coordinates. **Thecal ornamentation:** thecal wall thin to thickened with longitudinal ridges; lists and spines absent, or listing varies from a small list in the angle between the base of the hypotheca and the left horn, to the occurrence of smooth- or slightly unevenly-margined lists along both sides of the proximal part of the apical horn, extending onto the epitheca; and along the base of the hypotheca, extending onto the proximal part of the left horn, and sometimes onto the base of the right horn, with a few spines supporting the left horn list in the region of recurvature; sometimes there is a list along the proximal part of the upper suture of the left horn. (See Fig. 5 A, B, E.)

Dimensions: *From the literature:* Jørgensen (1911), girdle diameter 74–85 μ ; length hypotheca 43–48 μ ; length apical horn 160–420 μ .

Distribution: This geographical variety is confined to the Mediterranean.

Jørgensen (1911) included his new species "*C. pavillardii*" in his Subsection *Vultur*, but omitted any comments on chain formation, merely giving the length of the apical horn as 160–420 μ . He noted that "*C. pavillardii*" could be confused with *C. vultur* and "*C. sumatranum*" from which it was distinguished by the very short, almost absent, basal part of the left horn. According to him,

"*C. pavillardii*" differed further from "*C. sumatranum*" in the longer more steeply sided epitheca, thecal ornamentation, and the less spreading horns. In 1920, Jörgensen observed that chains of "*C. pavillardii*" were relatively very frequent in his Mediterranean samples, and referred to Schröder's figure of a three-celled chain of "*C. tripos* var. *macroceras* f. *undulata*" from the Gulf of Naples. He also suggested that specimens from near Sicily listed as "*C. vultur*" by Cleve (1903), were in fact "*C. pavillardii*". Böhm (1931a) commented that chains were rarely found in the Adriatic, and recorded a greater percentage of short-apical-horned cells in winter.

Schröder's poor figure is the only published illustration of a chain of var. *pavillardii*. Here, the apical horns of the two posterior cells are about 0,25 the length of the apical horn of the anterior cell, as is typical of Subsection *Robusta*, but the ratio of the length of the apical horn to that of the body in the posterior cells is 1,5 and 1,9, which is higher than that recorded in other chains of this Subsection. This ratio is 1,4 in Böhm's figure of a short-apical-horned winter form.

The available evidence provides no sound justification for the separation of "*C. pavillardii* Jörg." as a distinct species from "var *sumatrana* Karsten". The fact that the former is the only morphological form of *C. vultur* recorded from the Mediterranean, where it appears to show relatively little variation, indicates that it should be treated as a geographic variety confined to this Sea, while specimens of *C. vultur* with the same abrupt recurvature of the left horn from other waters, are treated as belonging to f. *sumatranum*.

There are some minor differences between the latter and the Mediterranean var. *pavillardii*: prominent lists with markedly serrate or denticulate margins have not been depicted in figures of var. *pavillardii*, the ratio of the length of the epitheca to that of the hypotheca is more commonly 1,0 in var. *pavillardii* than in f. *sumatranum*, where it is mostly < 0,8, (see Fig. 9); the girdle diameter appears to be slightly larger in var. *pavillardii*, but the only measurements available are those of Jörgensen (1911).

Specimens referred to as "*C. pavillardii* Jörg." have been recorded outside the Mediterranean by Jörgensen (1911, 1920), from Atlantic, Indian and Pacific waters; by Steemann Nielsen (1939), in Indian and East Asian waters, with the same ecology and distribution as *C. vultur*; by Gaarder (1954), who noted chain formation, from the Atlantic, and by Graham and Bronikowsky (1944), who were the first to treat the taxon "*pavillardii*" as a variety of *C. vultur*. Sournia (1967) commented that this treatment was excessive. The only illustration of a specimen referred to by the epithet "*pavillardii*" from a locality outside the Mediterranean is that of Graham and Bronikowsky.

In the NGY samples, two specimens were found with long apical horns, which corresponded to Graham and Bronikowsky's figure, (see Fig. 8A-C).

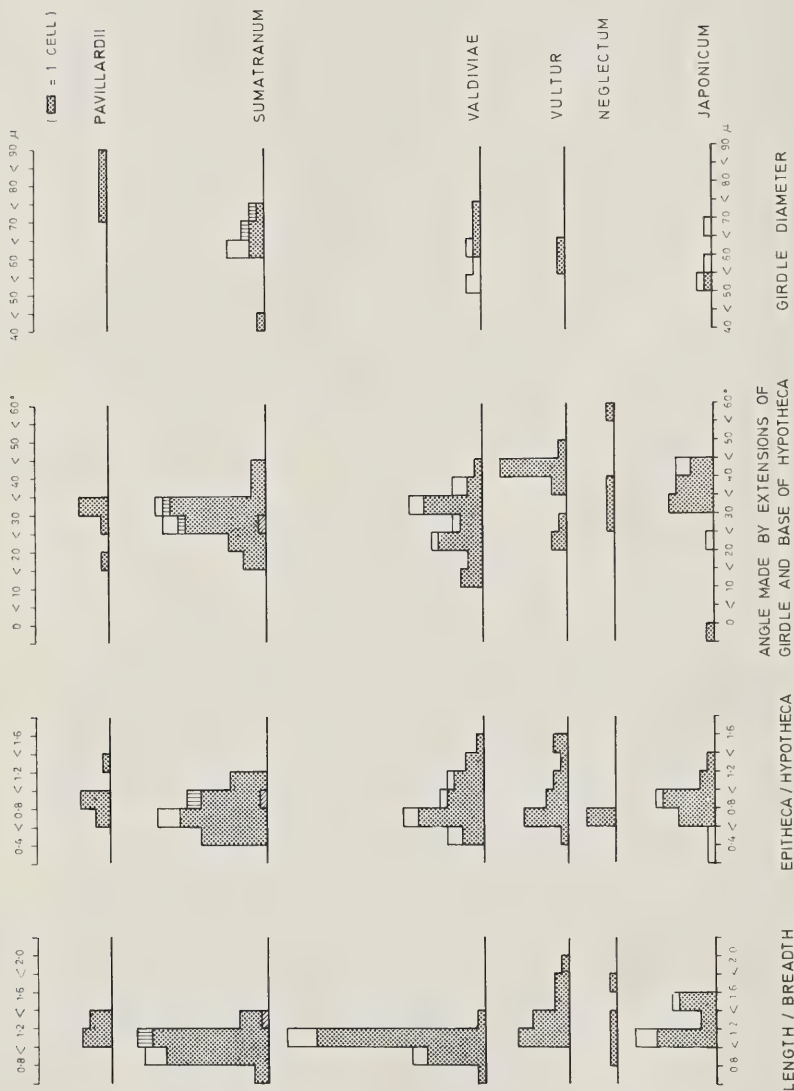


FIG. 9.

Histograms showing variation in body shape in *C. vultur*: the dotted shading refers to specimens from the literature, the white to NGY specimens, the diagonal hatching to Graham & Bronikowsky's figure of "*C. vultur* var. *pavillardii*" (1944, fig. 23C, = *f. sumatranum*), and the vertical hatching to the NGY specimens of *f. sumatranum* which resemble it. (Dimensions of girdle diameter given in the literature by Jørgensen (1911), Nie (1936) and Klement (1964).)

All three differed from specimens of *var. pavillardii* depicted in the literature and other specimens of *f. sumatranum*, with regard to antapical horn curvature, only in the curvature of the right horn, where the MRC occurred between the 45 and 75 μ radius coordinate. In one NGY specimen, lists were absent from the antapical horns, but the proximal parts were denticulate along the lower sutures, with four of the denticles enlarged into spines in the region of recurvature of the left horn.

Ceratum recurvum (Jørgensen) Reinecke stat. nov.

C. sumatranum var. *recurvum* Jørgensen (1911): 74, Pl. 9, Fig. 156.

C. vultur var. *recurvum* (Jörg.) Graham & Bronikowsky (1944): 41, Fig. 23A.

C. vultur var. *sumatranum* f. *recurvum*: Schiller (1937): 419, Fig. 460c.

C. vultur f. *recurvum*: Sournia (1967): 483, Fig. 97.

C. vultur var. *sumatranum* "Endglied einer Kette" Steemann Nielsen (1934): 27, Fig. 66.

C. triplos buceros: Karsten (1907) p.p.: 409, Pl. 51, Fig. 8.

Diagnosis: Differs from the specimens of *C. vultur* with recurved antapical horns, in that a marked recurvature of the left antapical horn occurs in all cells, not just the posterior members of a chain; this recurvature occurs between the 45 and 75 μ radius coordinates, not beyond the 120 μ radius coordinate; the left horn is markedly angled at the point of recurvature, not gradually recurved, and does not extend beyond the 120 μ radius coordinate. Differs from *C. reflexum* in that the left horn degree coordinate at the point of recurvature exceeds 90°. (See Figs. 4, 6J, K and 7G.)

Description: *Antapical horn curvature:* The *left horn* degree coordinate with the 15 μ radius coordinate is generally 60–70°, (87° in the specimen figured by Graham and Bronikowsky l.c.); the MRC occurs between the 15 and 45 μ radius coordinates and is about 20°; the horn is recurved posteriorly between the 45 and 75 μ radius coordinates; at the point of recurvature the horn is "angled" and the thecal wall of the recurved part is thinner; the horn is short, not exceeding the 120 μ radius coordinates; the distal part may lie roughly parallel to the base of the hypotheca, or be directed posteriorly so that the horn tip is posterior to the point of inception of the horn. The *right horn* degree coordinate with the 15 μ radius coordinate is usually less than that of the left; the MRC occurs between the 15 and 30 μ radius coordinates and is less than that of the left horn; the distal part may be recurved, this recurvature being gradual or "angled"; when there is no recurvature, a slight kink may be present at about mid horn length, when the thecal wall suddenly becomes thinner; the right horn may extend to a longer radius coordinate than the left horn. Narrow *lists* with smooth or serrated margins may be present at the base of the apical horn, and a list may occur at the angle between the left side of the hypothecal

base and the base of the left horn; the proximal part of one or both antapical horns may be slightly spinose along the posterior edge. Two-celled chains have been recorded; the length of the apical horn of the posterior cell and of short-apical-horned single cells is about half that of the body; in long-apical-horned anterior and single cells, the length of the apical horn is 2.2–3.1 times that of the body; the length of the apical horn of the posterior cell of a chain is about 0.2 that of the anterior cell. The body is about as broad as long.

Dimensions: In two specimens examined: Girdle diameter 57 μ ; length hypotheca 36–39 μ ; length epitheca 18–24 μ ; length apical horn 162–172 μ . *From literature:* Jørgensen (l.c.), diameter 54 μ .

Distribution: Records scant, probably because it has been confused or included with *C. vultur*. It appears to be a very rare warm water species recorded from all oceans, but not found in the Mediterranean. Graham and Bronikowsky (l.c.) found it at only two stations in the Pacific, but common in the North Equatorial current of the Atlantic. (See Table 1.)

Steemann Nielsen (1934), who illustrated a posterior chain cell with a short apical horn, wrote: "Die »Varietät *v. recurvum* Jørgensen« wurde öfters als Endglieder von Ketten, bei denen die ersten Glieder typische *sumatranum* warend gefunden. Solche »*recurvum*« -Zellen können nur als Degenerationerscheinungen aufgefasst werden." Schiller (l.c.) published three figures of what he called the anterior, hind and end chain members of *C. vultur* var. *sumatranum*. The first two are Jørgensen's figures of anterior and posterior cell members of what he called "*C. sumatranum*", the last is Steemann Nielsen's figure of *C. recurvum*. Later workers thus accepted Steemann Nielsen's conclusion. Graham and Bronikowsky, who considered *C. vultur* as consisting of various forms with numerous intergrades, published no convincing evidence of intergrades between "*C. vultur* var. *recurvum*" and other forms of *C. vultur* with recurved left antapical horns.

In the specimens and figures of *C. recurvum*, apart from that of Steemann Nielsen, which has truncated antapical horns, the tips of the antapicals are tapered and closed, and the left horn does not exceed the 120 μ radius co-ordinate, while in *C. vultur*, the tips of the antapicals are often truncate, and in all specimens examined, including those with truncate tips, the left horn exceeds the 150 μ radius coordinate.

Although the species has been illustrated but five times, and only two specimens were found in the present survey, all cells recorded show a uniformity of the diagnostic characters sufficient to justify the recognition of this taxon as a distinct species.

Steemann Nielsen appears to have confused *C. recurvum* with posterior chain members of *C. vultur* f. *valdiviae* with recurved antapical horns, such as illustrated by Okamura (1907, Pl. 3, Fig. 1a, see Fig. 6H).

Subsection **Reflexa** (Jørgensen) Reinecke stat. nov.

Section *Reflexa* Jørgensen (1911): 87.

Diagnosis: Distinguished by the curvature of the left antapical horn, which is abruptly recurved before the 90° coordinate so that it lies posteriorly directed and approximately in line with the apical horn.

Ceratium reflexum Cleve (1900): 15, Pl. 7, Figs. 8, 9.

Karsten (1907): 414, Pl. 48, Fig. 9; Jørgensen (1911): 87, Pl. 10, Fig. 184; Pavillard (1931): 94; Steemann Nielsen (1934): 25, Fig. 74; (1939): 15; Schiller (1937): 420, Fig. 461; Graham & Bronikowsky (1944): 45, Fig. 27H; Wood (1954): 305; (1963a): 40, Fig. 149a, b; Sournia (1967): 486, Fig. 99; *non* Silva (1955): 172, Pl. 9, Fig. 9 (= deformed specimen of an unidentifiable species belonging to Subsection *Macroceras*).

"*C. reflexum* Cleve forma" Schröder (1906): 366, Fig. 39.

C. vultur var. *productum* Wood (1963b): 16, Fig. 53.

Description: *Antapical horn curvature:* The left horn degree coordinate with the 15 μ radius coordinate is about 60°, the rate of change from the 15 to the 30 μ radius coordinate is <10°, and between the 30 and 45 μ radius coordinates, the horn begins a very gradual recurvature backwards, so that its distal part lies posteriorly directed almost in line with the apical horn; the proximal part of the horn is fairly broad, at the point of recurvature it may be slightly "angled", then it tapers to the tip. The right horn degree coordinate with the 15 μ radius coordinate generally exceeds that of the left horn; the degree coordinate with the 30 μ radius coordinate is > 90° and the MBC radius coordinate is short, being < 15 μ ; the distal part is generally not as slender as that of the left horn. The apical horn may be broad at its base or well delimited from the epitheca at inception. Lists with smooth to serrate margins may occur along the base of the hypotheca and the adjacent bases of the antapical horns, sometimes also along the base of the upper suture of the left horn, and along both sides of the base of the apical horn, which may instead be ornamented with spines. The body is as broad as long to about 1,3 times as long as broad. The ratio of apical horn: body length varies from 1,8—3,0. (See Figs. 6S and 7H.)

Apart from specimens with truncate antapical horns depicted by Steemann Nielsen (1934) and Wood (1963a), the antapical horns of all specimens illustrated in the literature and the single specimen found in the present survey, end in a tapered tip, and do not exceed the length of the apical horn, being about greater than or equal to half its length. There is no record of the occurrence of chains in this species.

Dimensions: In single specimen examined: Girdle diameter 54 μ ; length body 63 μ ; length hypotheca 42 μ ; length epitheca 15 μ ; length apical horn 192 μ .

From literature: Jörgensen (l.c.), girdle diameter 55–58 μ ; length hypotheca 37–43 μ ; length of apical horn 170–220 μ .

Distribution: A very rare warm water species, recorded from all the oceans, but not the Mediterranean. Graham and Bronikowsky (l.c.) classify it as "intolerant, tropical . . . probably a shade species". (See Table 1.)

Jörgensen considered that there was a distinct relationship between *C. reflexum* and what he called *C. sumatranum* var. *recurvum*. There is some similarity in the relative shortness of the antapical horns, the recurvature of the left horn, and, in the NGY specimens, the left profile of the hypotheca. Although the curvature of the left horn in a specimen depicted by Cleve (l.c. Fig. 8), is such that it forms an oblique angle, rather than a straight line, with the apical horn, no true intermediates between the two have yet been recorded.

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Radius coordinates in radius units

5 10 15 20 25 30 35 40 45 50

MASSILSENSE

97	102	109	116	123	133	140.5	146.7	151	155	89.55	1.38	86.62	1.67	-0.01	93.91	0.38	0.05	-0.0007		
80	100	108	115.5	123	130	136.3	141	144.7	147.8	87.87	1.30	73.97	2.09	-0.01	80.70	1.96	-0.01	-0.0001		
80	90	103.5	110.5	120.5	129.5	134.5	139	142	145	78.43	1.57	68.06	2.61	-0.02	69.07	2.43	-0.01	-0.0001		
77	84	92	102	112	121	128.5	133.5	138	141	71.23	1.52	63.15	2.33	-0.01	70.65	1.90	0.04	-0.0007		
77	84	96	107	116	124	130.5	135	139	143	74.20	1.50	63.49	2.57	-0.02	66.43	2.05	0.00	-0.0003		
75	88	103	116	126	133	139	143	147	150	76.25	1.55	52.12	2.64	-0.02	64.83	2.16	0.00	-0.0003		
70	79	88	100	114	125	135	143	150	155	60.73	2.01	53.82	2.45	-0.01	63.37	1.90	0.00	-0.0002		
70	79	88	100	114	125	135	143	150	155	55.63	2.38	24.92	5.75	-0.06	30.85	4.40	-0.01	-0.0006	63.40	-0.0171
78.1	87.5	99.2	111	121.6	130.4	137.3				74.88	1.66	61.81	2.96	-0.02	65.93	2.23	0.01	-0.0004		0.0002

TRICHOCHOS Diam. less than or equal to 42 μ

125	136	144	151	155	89.55	1.38	86.62	1.67	-0.01	93.91	0.38	0.05	-0.0007							
66	72	82	91	103	114															
66	72	84	94	103	114	67.13	1.69	65.68	0.84	0.02	68.07	0.41	0.03	-0.0002						
74	77	81	84	86.5	89	53.17	0.70	64.92	0.53	0.00	60.22	2.40	-0.07	-0.0009						
61	69	75	84	87	90	63.23	0.83	64.98	0.66	0.00	55.18	2.42	-0.06	0.0009						
50	60	65	69	73	77	44.57	1.17	50.68	0.78	0.01	50.43	2.42	-0.06	0.0009						
62	69.5	73.3	78.5	83.3	89.9	51.68	1.43	60.85	0.51	0.02	57.86	1.04	-0.01	0.0002						

TRICHOCHOS Diam. greater than or equal to 45 μ

119	129	135.5	141	147	156.6	162.7	168.1	172.9	176.75	0.11	0.02	79.57	-0.39	0.04	-0.0003					
78	84	88	92	99	107	115	123	131	138	64.50	1.33	76.75	-0.12	0.03	80.54	-0.75	0.06	-0.0003		
77	80	83	87	92	98	105	112	119	126	60.07	1.57	76.98	-0.12	0.03	80.54	-0.75	0.06	-0.0003		
74	76	79	85	91	98	111	133	143	147	54.63	1.79	72.55	-0.00	0.03	84.33	2.07	0.07	-0.0003		
73.9	76.9	80.7	86.2	92.7	100.7	112	128	141	147	54.45	1.78	68.81	0.35	0.03	74.01	-0.57	0.07	-0.0005	62.22	0.0103
										56.78	1.70	72.09	0.16	0.03	76.04	-0.54	0.06	-0.0004	66.74	0.0044

MACROCEROS From Norway

50	54	67	80	103	121	135	146	153	159	31.73	2.73	24.57	3.44	-0.01	49.47	-0.97	0.18	-0.0023		
44	48	54	63	75	89	107	120	130	138	23.50	2.30	32.75	1.38	-0.02	49.78	-0.97	0.18	-0.0023		
40.2	46.1	56.9	72.5	97.9	121	132.4	145.6	152.7	156.6	23.41	2.81	15.60	3.58	-0.01	36.02	-0.04	0.14	-0.0019		
										20.77	2.96	11.55	3.88	-0.02	42.00	-1.52	0.21	-0.0028		

MACROCEROS NGY Specimens

39	50	82	103	113	121.3	127	133	137	141	42.55	2.26	10.20	5.49	-0.06	2.91	6.79	-0.11	0.0007	21.95	1.93
35	43	60	83	95	104	110	115	121	126	31.37	2.11	10.24	4.22	-0.04	12.52	3.84	-0.11	0.0007	21.95	1.93
35	43	60	83	95	104	110	115	121	126	33.45	1.79	12.68	3.80	-0.04	14.33	3.47	-0.02	0.0007	21.95	1.93
33	42	60	75	88	92	97	105.7	109.3	112.3	33.45	1.79	12.68	3.80	-0.04	14.33	3.47	-0.02	0.0007	21.95	1.93
36.8	49.2	72.8	89.6	100.4	115.7	121.7	127.5	126.1	127.5	38.72	2.04	12.74	4.04	-0.05	10.35	4.96	-0.06	0.0002	22.70	1.95

DEFLEXUM

58	62	72	95	128	145	155	162	167	171	42.33	2.89	23.00	4.82	-0.04	56.71	-1.16	0.22	-0.0021	97.35	1.93
55	65	82	104	124	137	144.7	151	159	165.5	46.89	3.17	5.70	7.29	-0.04	36.55	2.85	0.05	-0.0011	97.35	1.93
55	65	82	104	124	137	144.7	151	159	165.5	46.89	3.17	5.70	7.29	-0.04	36.55	2.85	0.05	-0.0011	97.35	1.93
44	53	78	103	129	145	155	161	166.5	170.7	43.79	2.86	18.64	5.58	-0.05	38.38	-2.09	0.31	-0.0049	97.35	1.93
52.5	59.3	73.7	106	137.1	151.3	165.7	169.7	169.7	172.9	41.76	3.02	10.00	6.20	-0.06	35.98	1.59	0.14	-0.0024	83.23	1.93

C₁ VULTUR F. SUMATRANUM

90	104	115	122	127	132	135	139	143	147	88.53	1.29	69.95	3.15	-0.03	51.76	6.38	-0.17	0.0017	37.39	10.09
										93.20	1.23	81.03	2.45	-0.02	73.73	3.75	-0.08	0.0007		

POLAR COORDINATES

APPENDIX TABLE I. Showing polar coordinates and regression coefficients calculated using a Polynomial Regression program for the portion of the left antapical horn between radius coordinates of 15 μ and 150 μ , in a selection of specimens of Section *Mariceros*. All specimens are from the same locality, and the specimens are grouped in taxa of unspecified rank, approximating those previously described in the literature. The intercept equals approximately 54 μ . Int. = intercept; underlined figures represent the mean degree coordinates calculated for each radius coordinate for all specimens examined, and the resultant polynomial regressions.

RESULTANT POLYNOMIAL REGRESSIONS

MACROCEROS NGY Specimens

39	50	82	103	113	121.3	127	133	137	141	42.55	2.26	10.20	5.49	-0.06	2.91	6.79	-0.11	0.0007	21.95	1.93
35	43	60	83	95	104	110	115	121	126	31.37	2.11	10.24	4.22	-0.04	12.52	3.84	-0.11	0.0007	21.95	1.93
35	43	60	83	95	104	110	115	121	126	33.45	1.79	12.68	3.80	-0.04	14.33	3.47	-0.02	0.0007	21.95	1.93
33	42	60	75	88	92	97	105.7	109.3	112.3	33.45	1.79	12.68	3.80	-0.04	14.33	3.47	-0.02	0.0007	21.95	1.93
36.8	49.2	72.8	89.6	100.4	115.7	121.7	127.5	126.1	127.5	38.72	2.04	12.74	4.04	-0.05	10.35	4.96	-0.06	0.0002	22.70	1.95

DEFLEXUM

58	62	72	95	128	145	155	162	167	171	42.33	2.89	23.00	4.82	-0.04	56.71	-1.16	0.22	-0.0021	97.35	1.93
55	65	82	104	124	137	144.7	151	159	165.5	46.89	3.17	5.70	7.29	-0.04	36.55	2.85	0.05	-0.0011	97.35	1.93
55	65	82	104	124	137	144.7	151	159	165.5	46.89	3.17	5.70	7.29	-0.04	36.55	2.85	0.05	-0.0011	97.35	1.93
44	53	78	103	129	145	155	161	166.5	170.7	43.79	2.86	18.64	5.58	-0.05	38.38	-2.09	0.31	-0.0049	97.35	1.93
52.5	59.3	73.7	106	137.1	151.3	165.7	169.7	169.7	172.9	41.76	3.02	10.00	6.20	-0.06	35.98	1.59	0.14	-0.0024	83.23	1.93

C₁ VULTUR F. SUMATRANUM

90	104	115	122	127	132	135	139	143	147	88.53	1.29	69.95	3.15	-0.03	51.76	6.38	-0.17	0.0017	37.39	10.09
										93.20	1.23	81.03	2.45	-0.02	73.73	3.75	-0.08	0.0007		

APPENDIX TABLE 2. SHOWING VARIATION IN POLAR COORDINATES IN SPECIMENS OF *CERATIUM VULTUR* SELECTED FROM THE LITERATURE

TAXON	MAY. RATE OF CHANGE OVER 5 R.U. AFTER INITIAL CHANGE FROM 0-5 R.U.				° COORDS AT POINT OF MAXIMUM BACKWARD CURVATURE				LEFT HORN ° COORDS				LITERATURE REFS.	
	Position along horn		Rate in °		Degree		Radius		coords		at			
	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	at 10 R.U.	at 30 R.U.		at 50 R.U.
F. VULTUR	15-20	10-15	28	15.5	50	70	57.5	77	7.5	12.5	53	126	146	Cl. (1900) Pl. 7, fig. 4
{ F. VULTUR F. VULTUR F. VULTUR	30-35	10-15	12.5	12	77	57	80	67.5	10.7	13.0	78	113	153	Pa. (1931) Pl. 3, fig. 8
	15-20	—	17	—	63	—	72.5	—	—	10.0	72.5	127	154	
	25-30	5-10	13	20	40	67	54	70	5.5	21.0	40	75	105	
{ F. JAPONICUM F. VULTUR	20-25	5-10	78	26	43	80	53	75	4.0	19.5	43	155	181	K. (1907) Pl. 48, fig. 13a
	15-20	5-10	30	22.5	65	80	71	75	4.0	11.5	68	147	169	
	5-10	5-10	21	24	57	45	63	55	7.5	6.5	78	133	165	J. (1911) Pl. 8, fig. 151a
{ F. VULTUR	15-20	5-10	19.5	10.5	57	77	72	78	6.5	11.5	68	127	156	
	30-35	5-10	63	23	54	80	61	75	4.0	23.0	55	77	175	Schr. (1906) Fig. 33c
	25-30	15-20	48	17	23	50	40	62	11.0	24.7	25	86	153	Schr. (1906) Fig. 31
F. JAPONICUM	15-20	5-10	72	30	50	45	58	55	7.5	14.5	52.5	164	185	O. & S. (1901) Fig. 17
F. JAPONICUM	20-25	5-10	45	13	60	86	68	83	3.8	13.5	65	155	184	G. & B. (1944) Fig. 23E
{ F. NEGLECTUM F. JAPONICUM	20-30	5-10	18	14	77	65	80	76	9.0	6.5	87	151	183	Bö. (1931b) Fig. 35b
	20-25	5-10	48	16	57	67	68	70	7.0	11.5	67	167	194	
F. NEGLECTUM	25-30	5-10	23	11	65	77	70	78	5.5	8.5	75	146	182	K. (1905) Pl. 19, fig. 12
F. NEGLECTUM	25-30	10-15	22	17.5	85	47	88	55	10.0	7.0	88	135	175	G. & B. (1944) Fig. 23F
{ F. VALDIVIAE F. VALDIVIAE F. VALDIVIAE	5-15	10-25	10	4	65	67	75	77	18.0	10.0	75	112	137	K. (1905) Pl. 19, fig. 12a
	5-10	10-20	14.5	2	58	56	71	73	20.0	8.5	75	113	132	
	5-10	10-20	14.5	2	58	77	72.5	83	28.0	10.0	72.5	111	132	
{ F. VALDIVIAE F. VALDIVIAE	5-10	10-15	20	10	65	60	73	68	11.3	7.0	85	133	151	K. (1907) Pl. 48, fig. 14a
	10-15	5-10	16.5	10	60	60	67.5	72	11.5	10.0	67.5	122	142	
	10-15	10-20	18	10	75	43	77	60	17.0	7.8	84	137	162	K. (1907) Pl. 48, fig. 14b
{ F. VALDIVIAE	5-10	5-10	15	9	55	70	65	75	8.0	9.5	68	113	128	
{ F. VALDIVIAE F. VALDIVIAE F. VALDIVIAE	5-10	10-15	26	9	50	80	60	84	9.0	6.5	76	127	151	Ok. (1907) Pl. 3, fig. 1a
	5-10	5-10	14.5	11	68	67	70	75	8.0	6.5	82.5	122	138	
	10-15	5-10	24.5	17	68	60	72	65	7.5	6.0	88	135	141	
F. VALDIVIAE	5-10	5-10	29.5	12	58	58	63	67	8.5	6.0	87.5	128	136	
F. VALDIVIAE	5-10	10-15	24	12	70	50	73	64	12.0	5.7	94	143	170	J. (1911) Pl. 8, fig. 153
F. VALDIVIAE	10-15	10-15	17.5	6	75	75	77	80	12.0	7.0	87.5	141	160	G. & B. (1944) Fig. 23H
F. VALDIVIAE	10-15	5-15	20	5.5	53	57	63	72.5	20.0	7.5	72	125	44	G. & B. (1944) Fig. 23D

APPENDIX TABLE 2. SHOWING VARIATION IN POLAR COORDINATES IN SPECIMENS OF CERATIUM VULTUR SELECTED FROM THE LITERATURE (continued)
TAXON MAX. RATE OF CHANGE OVER 5 R.U. AFTER INITIAL CHANGE ° COORDS AT POINT OF MAXIMUM BACKWARD CURVATURE LEFT HORN ° COORDS LITERATURE REFS.

TAXON	Position along horn		Rate in °		° COORDS AT POINT OF MAXIMUM BACKWARD CURVATURE		° COORDS AT		° COORDS AT		LITERATURE REFS.
	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	
F. SUMATRANUM	10-15	5-10	25	15	78	75	78	76	5,0	95	155 170
{ F. SUMATRANUM	5-10	21,5	21	21,5	75	59	75	63	5,0	96,5	149
{ F. SUMATRANUM	5-10	29	18	43	74	74	52	74	5,0	72	143
{ F. SUMATRANUM	10-15	5-10	46	32	58	50	67	55	8,0	86	163
{ F. SUMATRANUM	10-15	35,5	22	35,5	70	60	68	65	4,8	102	166
{ F. SUMATRANUM	5-10	25,5	70	70	63,5	68	58	58	4,5	105	162
{ F. SUMATRANUM	5-15	5-10	35	10	50	70	60	72	8,5	85	141
{ F. SUMATRANUM	5-10	35	13	77	67	78	73	73	5,5	112	150
{ F. SUMATRANUM	5-10	28	10	90	75	73	77	77	3,0	118	169
{ F. SUMATRANUM	5-10	21	14,5	95	78	85	75	75	3,5	113	163
{ F. SUMATRANUM	10-15	27,5	15	85	80	80	78	78	4,0	112,5	158
{ F. SUMATRANUM	10-15	28,5	10	72,5	77	70	85	85	2,0	102,5	161
{ F. SUMATRANUM	10-15	28	10	75	68	80	75	75	5,0	96	165
{ F. SUMATRANUM	5-10	30	12,5	90	68	73	82	82	2,5	120	165
{ F. SUMATRANUM	5-10	28	13	70	85	73	65	65	4,0	94	167
{ F. SUMATRANUM	10-15	26	18	70	70	73	65	65	5,0	94	167
{ F. SUMATRANUM	5-10	36	8	93	105	87	90	90	0,0	4,5	166
{ F. SUMATRANUM	5-10	15	7	83	88	85	86	86	4,5	5,5	171
{ F. SUMATRANUM	10-15	24	15	85	75	64	75	75	8,5	75	157
{ F. SUMATRANUM	5-10	28	15,5	85	72	83	72	72	5,0	113	159
{ F. SUMATRANUM	5-10	35	16	55	60	62	66	66	6,0	90	155
{ F. SUMATRANUM	5-10	35	15	70	58	70	68	68	8,0	105	145
{ F. SUMATRANUM	5-10	35	10,5	65	67	67,5	72	72	7,5	100	156
{ F. SUMATRANUM	10-15	32	25	75	45	75	57	57	4,5	105	165
{ F. SUMATRANUM	10-15	21	20	87	58	80	65	65	3,5	107	158
F. SUMATRANUM	5-10	49,5	16	73	58	70	68	68	8,5	122,5	155
F. SUMATRANUM	5-10	15-25	22,5	6	95	77	75	80	4,0	117,5	144
V. PAVILLARDII	5-10	5-20	37,5	8	85	77	63	80	3,5	122,5	156
V. PAVILLARDII	5-10	5-10	33	14	85	93	80	80	2,0	118	149
V. PAVILLARDII	5-10	5-10	20	5	105	90	90	85	0,0	125	154
V. PAVILLARDII	5-10	10-15	42	12	73	55	73	67	11,5	115	162
									5,0	115	177

The figures were photographed and printed at approximately the same scale as the camera lucida drawings of the NGY specimens. These measurements are subject to some error. (R.U., radius unit, one radius unit is approximately equal to 3 μ ; brackets indicate individuals of a chain; * indicates value estimated. Radius coordinates given in R.U.)

APPENDIX TABLE 3. SHOWING THE RELEVANT POLAR COORDINATES USED TO CLASSIFY SPECIMENS OF *CERATIUM VULTUR* FOUND IN AGULHAS CURRENT NGY SAMPLES, WITH A KEY TO THE TAXA FOUND

	MAX. RATE OF CHANGE OVER 5 R.U. AFTER INITIAL CHANGE FROM 0-5 R.U.				° COORDS AT 5 R.U.				POINT OF MAXIMUM BACKWARD CURVATURE				LEFT HORN° COORDS			
	Rate in °		L. Horn		R. Horn		L. Horn		R. Horn		L. Horn		R. Horn		L. Horn	
	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn	L. Horn	R. Horn
F. SUMATRANUM	Position along horn		Rate in °		L. Horn		R. Horn		L. Horn		R. Horn		L. Horn		R. Horn	
	5-10	15-20	15	6	90	60	70	70	70	70	12.0	4.5	105	134	105	134
	5-10	15-20	37	17	88	57	70	70	70	70	17.0	3.0	104	132	104	132
	5-10	15-20	34	12	88	57	70	70	70	70	17.0	3.0	122	137	122	137
	5-10	15-20	39	13	77	59	73	63	63	63	7.0	4.5	116	157	116	157
F. VALDIVIAE	5-10	5-10	38	20	70	65	74	70	70	70	6.5	6.0	108	155	108	155
	5-10	10-15	21	14	60	45	62	62	62	62	11.5	5.2	81	141	81	141
	5-10	5-10	27	12	52	50	60	69	69	69	13.0	6.5	79	130	79	130
	5-10	5-10	25	11	59	48	67	72	72	72	17.0	9.5	84	134	84	134
	5-10	10-15	22.5	14	60	55	60	62	62	62	5.0	5.0	86.5	136.5	86.5	136.5
F. JAPONICUM	5-10	5-10	26	10.5	60	37	63	*	*	*	—	6.0	86	129	86	129
	20-25	5-10	59	25	70	90	74	80	80	80	3.5	14.0	72.5	181	72.5	181
	15-20	5-10	58	29	57	68	70	70	70	70	5.5	14.5	66	173	66	173
	15-20	5-10	57	23	55	67	67	73	73	73	6.5	13.7	60	172	60	172

(**) indicates right horn directed laterally or approximately parallel to base of hypotheca after inception;
* indicates right horn recurved posteriorly after inception; brackets indicate chain of two cells.

KEYS TO SPECIMENS FOUND:

- (1) Left horn degree coordinate with 10 R.U. greater than 100°
- (2) Left horn degree coordinate with 10 R.U. less than 100°
- (i) Left horn MRC greater than 50°, left horn MBC radius coordinate greater than 10 R.U.
- (ii) Left horn MRC less than 50°, left horn MBC radius coordinate less than 10 R.U.

F. SUMATRANUM
F. JAPONICUM
F. VALDIVIAE

***ALOE CHLORANTHA*: A NEW SPECIES FROM THE SOUTH WESTERN KAROO (SOUTH AFRICA)**

J. J. LAVRANOS

ABSTRACT

The discovery, in the South Western Karoo of the Cape Province, of a new *Aloe* is reported upon. The plant in question is established as a *species nova* and its affinities are discussed in some detail.

UITTREKSEL

ALOE CHLORANTHA: 'N NUWE SOORT VANAF DIE SUID-WESTELIKE KAROO (SUID-AFRIKA).—Die ontdekking in die Suid-Westelike Karoo van die Kaap-provinsie van 'n nuwe *Aloe* soort word verslag oor gedoen. Die soort word 'n *species nova* geag en sy verwantskap word volledig bespreek.

INTRODUCTION

Towards the end of 1970, Mr. Elias Buhr mentioned to the author the presence, in the Sutherland district, of an *Aloe* which he thought might be undescribed. Specimens of this plant had been brought to him by Mr. W. J. Theron.

On the 6th Sept. 1971, a visit was made to a farm situated some 40 km North-West of Sutherland, where a small number of plants (*Lavranos & Butler* 8877) were found growing among boulders on the Northern slope of a dolerite hill. At a distance these plants reminded one of *A. broomii* Schönl. which, too, is a denizen of dolerite outcrops but which has never been found West of Carnarvon and Beaufort West. Dry inflorescences found near these plants were, however, very different from those of *A. broomii* mainly in that they bore pedicels over 20 mm long and their racemes were much more laxly flowered and occupied only the apical third part of a total length of 1.60 m. It was fairly obvious that we were dealing with something hitherto unrecorded but the absence of flowering material made any diagnosis impossible.

During a visit to Grasberg, near Nieuwoudtville, early in 1972, Dr. B. D. H. van Niekerk, of Randburg, recognised the Sutherland plants growing in Mr. Buhr's garden as apparently the same as an *Aloe* which occurs in some numbers not far South of Fraserburg, on the farm Klipheuwel, property of Mr. O. G. Mans. Dr. van Niekerk had known these plants and been intrigued by them for some years but, not having seen them in flower, he too had been left guessing as to their identity.

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FIG. 1

Plant in typical habitat among dolerite boulders.

It was decided that Dr. van Niekerk and the author should visit the Fraserburg locality when the aloes came into flower. This was done on the 14 Oct. 1972 and Mr. Buhr, Mr. Stayner of the Karoo Garden and Mr. Dumoulin of the Department of Nature Conservation joined the party.

Some of the plants were indeed flowering but, on account of the prolonged drought, most inflorescences had been eaten by thirsty dassies (*Procavia capensis*) as they are very juicy and not too bitter. It was immediately apparent that these aloes represented a hitherto unrecorded species.

A narrow valley between boulder strewn dolerite slopes was the habitat of these plants which were absent from South facing localities and showed a predilection for warm, North facing positions. Vegetatively, they were quite

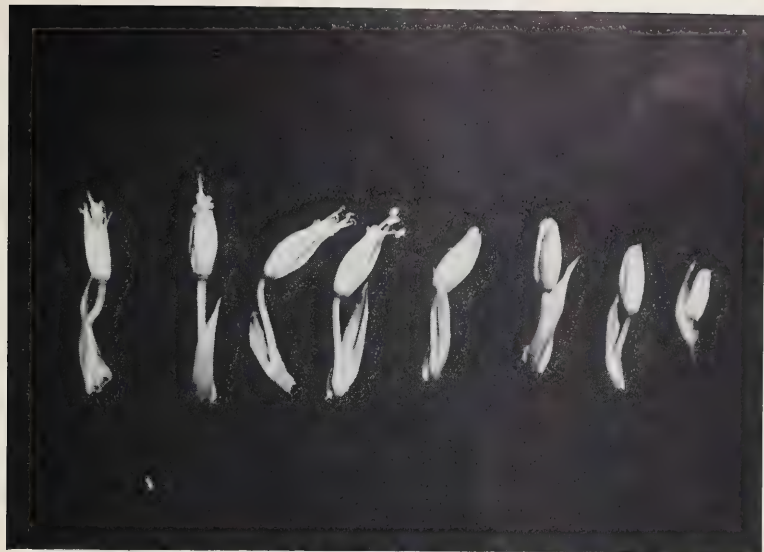


FIG. 2
Flowers 1/1 from bud to post-pollination stage.

indistinguishable from those which had been observed at Sutherland and, here too, they were not at all common.

It was noticed that, after reaching a certain size, the rosettes divide, forming groups of up to 10, although 2 to 4 is a more usual number. Very few young plants were seen and it was found that many of the older specimens had either died or were affected by an insect, the larva of which eats into the centre of the crown of leaves, eventually killing the whole plant.

DESCRIPTION

Aloe chlorantha Lavranos nov. sp., *A. broomii* Schonland affinis sed inflorescentia graciliore, racemis laxiore florentibus, floribus dimidio minoribus, a 20 mm pedicellatis satissime discedit.

Planta perennis, succulenta, acaulis sed saepe caule procumbenti, a 1,50 m longo munita, singularis sed per divisionem in usque a 10 multiplicans; *foliis* rosulatis, deltoideis, acutis, leviter falcatis, a 40 cm longis, basi a 8 cm latis, coriaceis, *supra* sensim vernicosis, planis vel leviter convexis, plus minusve striatis, viridibus vel brunescens, *subtus* facie superiori similibus sed saepe albomaculatis; *marginibus* foliorum cartilagineis fuscis brunneo-rubris, aculeis deltoideis, rigidis, 2 mm longis, 10—30 mm inter se distantibus munitis; *inflores-*



FIG. 3

Portion of raceme showing nutant habit of open flowers.

centiis usque a 3 ex eadem capitem productis, a 160 cm altis, simplicibus sed rarius bifurcatis; *pedunculo* basi plano-convexo, a 20 mm lato, supra tereti, bracteis sterilibus, a 25 mm longis abundanter induto; *racemis* a 35 cm longis, modice densifloris, gemmis juvenibus per bracteas earum occultis, floribus apertis nutantibus; *bracteis* 12 a 20 mm longis, 5—8 mm latis, ovatis deltoideis, acutis, carnosis, flavo-viridibus, multinerviis; *pedicellis* teretibus, 15—22 mm longis, semper erectis et pedunculo quasi adpressis; *perigonii*s ventricosus, stipitatus, flavo-viridibus, 10 mm longis, 4 mm diam., segmentibus exterioribus usque a basin liberis, flavo-viridibus, nervis 6—8, laete viridibus, apice confluentibus, per longitudinem percursis, segmentibus interioribus ad exteriores similibus sed angustioribus; *filamentis* flavescentibus, antheris aurantiacis deinceps per 3 mm exsertis; *stylo* flavo, stigmati aetate per 4 mm exserto; *ovario* laete viridi.

Type material: Cape Province, 3121 CD (Fraserburg), on dolerite outcrops on the farm Klipheuwel, alt. appr. 1 400 m, *Lavranos* 10024 (PRE, holotype).

Plants perennial, succulent, stemless or often with a procumbent stem up to 1,50 m long, solitary or splitting into up to 10 rosettes; *leaves* rosulate, deltoid, acute, slightly facate, to 40 cm long, to 8 cm broad at base, leathery; upper surface almost vernicose, flat or slightly convex, more or less striate,

bright green shading into purplish; lower surface similar to the upper but often bearing white spots; margins cartilaginous, dark brown-red, armed with rigid, deltoid, sharp, dark brown-red teeth, which are 2 mm long and 10—30 mm distant; *inflorescences* up to 3 from each rosette, to 1,60 m high, simple or rarely forked; *peduncle* basally plano-convex and to 20 mm broad, terete above, covered with numerous deltoid, acute sterile bracts, up to 25 mm long; *racemus* to 35 cm long, moderately dense, the young buds covered by their bracts, the open flowers nutant; *bracts* 12 to 20 mm long, 5—8 mm wide, ovate deltoid, acute, fleshy, yellow-green, many-nerved; *pedicels* terete, 15—22 mm long, always erect and almost hugging the peduncle; *perianth* conspicuously small, only 10 mm long, 4 mm diam. at the middle, stipitate, narrowing to the mouth and tapering into the pedicel, yellow-green, the outer segments free to base, bearing 6—8 bright green, apically confluent, longitudinal nerves, the inner segments similar but apparently narrower than the outer; *filaments* yellowish, the orange anthers in turn exerted by 3 mm; *style* yellow, the stigma at length exerted by 4 mm; *ovary* bright green.

DISCUSSION

The closest relative of this new species seems to be *Aloe broomii* Schonl.—In both, the simple or rarely bifurcate peduncle is covered, virtually from the base up, by numerous, large sterile bracts which, like the floral ones, are rather fleshy. This character is met with in other South African species of *Aloe*, notably *A. glauca*, *A. pratensis*, *A. microstigma*, *A. comosa* etc. In *A. broomii* the raceme occupies well over one half of the total length of the inflorescence, while in *A. chlorantha* it is not longer than one third of the whole. The buds in both species are covered by the imbricate bracts but, in *A. chlorantha*, the conspicuously small flowers, when open, are entirely free and nodding, their pedicels, at 20 mm, being twice as long as the perianths and as long, at least, as the bracts. In *A. broomii*, the 20—25 mm long flowers are hidden by the bracts and face obliquely upward, the pedicels not being longer than 2 mm. Finally, in the new species, the anthers and stigma become exerted only by 3—4 mm, whereas in its relative they do so by 12—15 mm.

The rosettes of *Aloe chlorantha* have fewer leaves than those of *A. broomii*. The leaves of the latter are never spotted as they often are, on the lower surface only, in the new species where they are, moreover, lineate and very smooth, indeed almost vernicose as in some tropical species of *Aloe*.

Mr. Stayner suggests a certain resemblance between *A. chlorantha* and the decumbent form of *A. microstigma* Salm Dyck which is found in the Sutherland and Calvinia districts. The flowers, however, of this form in no way resemble those of the Fraserburg plants.

If flowers and inflorescence be a guide, a much closer relationship may exist between our species and *A. comosa* Marl. & Berger despite their widely differing appearance. Both species have, as a rule, simple inflorescences with copiously bracteate peduncles and large floral bracts which hide the buds. Their flowers are almost identical, proportions being guarded. It is possible that this relationship be as close as the more apparent one with *A. broomii*.

The reader may find it interesting to note that the type locality of *A. chlorantha* is only a few kilometres distant from that of Burchell's *A. claviflora*.

In the western portion of its range, *A. chlorantha* receives more than half of the rainfall in winter (April to October). At Fraserburg, the eastern limit, only one third of the total precipitation occurs in these months. The area North of Sutherland, where the new species was first found, gets about 200 mm of rain per annum while the corresponding quantity at Fraserburg is 165 mm.

It has been suggested by some that *Aloe chlorantha* might be of hybrid origin but this betrays total ignorance of hybridisation and its effects. The new species is wholly constant throughout its range, both in floral and vegetative characters. This is incompatible with the behaviour of a putative hybrid swarm. Furthermore, a hybrid presupposes the existence of two parent species. No *Aloe*, other than *A. claviflora* grows anywhere near *A. chlorantha* and is limited to the easternmost portion of the latter's range.

Shortly before his untimely death, Dr. G. W. Reynolds told the author that, in his view, there were far too many ill defined taxa among S. African aloes and that, were he to re-write his first book, he would reduce their numbers considerably. In this respect, too, *A. chlorantha* is a "good" species for, when in flower, its identity cannot be mistaken, whether in nature or in a garden. With its small, green flowers it is neither a beautiful nor a conspicuous plant, which would account for its late discovery.

ACKNOWLEDGEMENTS

The author wishes to express his appreciation and thanks to:

Mr. Elias A. Buhr for first drawing his attention to the existence of *A. chlorantha* and to him and Mrs. Buhr for hospitality at Grasberg on numerous occasions.

Dr. B. D. H. van Niekerk for guiding him to the type locality, for copious field notes and critical remarks concerning the affinities of the new species.

Mr. and Mrs. O. G. Mans of Klipheuwel, in the Fraserburg district for their hospitality and for allowing the collection of the type material on their farm.

Mr. J. S. Cloete, of the farm Drupfontein in the Sutherland district for permission to study the plants and collect material on his property.

Mr. W. J. Theron, for leading him to the Sutherland locality and for making available the first specimens from there.

BOOK REVIEWS

WESTERN CAPE SANDVELD FLOWERS by Hilda Mason. Text by Enid du Plessis, with pp. 203, 85 illus. Cape Town: Struik, 1972. R10.00.

The idea of producing this book was conceived some four years ago when Enid du Plessis, impressed by Hilda Mason's work as an artist, suggested that she should turn her attention to flower studies. The unique and fast disappearing flowers of the sandveld were in need of someone to record their glories before many of them disappeared forever. This was a challenge and the artist was not slow to take it up.

Not every artist is a good botanical painter but in this book Hilda Mason has shown that she has all the qualities needed. The result is a book that is not only an artistic achievement but is also a useful book for both botanist and layman. A sense of orderliness pervades the whole. As a frontispiece a map of the area is given. This is followed by an interesting account of the early explorers of the sandveld, written mainly by Professor Eric Axelsson, Hilda Mason's husband. A short account of the geological history and vegetation of the sandveld follows. The introduction concludes with some interesting observations made by Wilferd Duckitt of Oudepost, Darling, a man who combines most successfully the role of farmer and veld conservationist. His remarks on the needs of the sandveld will be appreciated by all who have at heart the welfare of this unique flora.

In the main part of the work the order of the plants is that adopted in the Flora of the Cape Peninsula by Adamson and Salter. As one opens the pages the text appears on the left hand side with the illustrations on the right. There are eighty-five plates. In but two cases does a single plant occupy a whole plate. In all the others several plants appear grouped together, well arranged and clearly numbered so that there is never any difficulty in relating the plants depicted to the text on the opposite page. The species are grouped in families, all authentically named by a number of botanical collaborators whose aid is acknowledged at the beginning of the work. Thus we have a book in which orderliness of presentation, authenticity of naming and excellence of illustrations combine to make it a reliable guide to the flora of the sandveld. The notes accompanying each species are commendably short and informative. The derivations of the plant names give an added interest.

Undoubtedly the importance of the work lies in its illustrations which are of high quality. They could only have been done by someone who loved the plants drawn and knew them as they grew. The difficulties encountered must have been enormous for many flowers are as temperamental as a prima donna. The fact that eighteen species of *Oxalis* have been depicted is in itself an achievement for most species of *Oxalis* will remain open only when the light is sufficiently intense, a condition not always compatible with the needs of the artist. Then too Hilda Mason has not confined her attention to the showy members of the flora. Inconspicuous or easily overlooked plants such as *Stoebe nervigera* or *Triglochin bulbosa* are there. The only families which have not received full attention are Gramineae and Cyperaceae. Perhaps this is too much to ask of the artist for even botanists tend to fight shy of these interesting but not very popular families.

This is a book to be treasured by botanist and laymen alike, in fact by anyone who has an interest in the sandveld and its flowers. It may well be that many of the flowers depicted may soon be extinct for the area is fast yielding to agricultural and industrial development. A showy plant such as *Echioschys spicatus* has not found a place in this book though the much less conspicuous *Echioschys incanus* is figured on page 163. Clearly Hilda Mason never saw the larger formerly common species with its spectacular woolly heads. Forty years ago it was a characteristic plant of deep sand and could not have been missed.

The printing is clear and reproduction of the plates is outstandingly good. Scattered in the text are small and delightful black and white drawings of scenes in the sandveld. A clear and accurate index concludes this admirable book.

M. R. LEVYN

INSTRUCTIONS TO CONTRIBUTORS TO THE JOURNAL OF SOUTH AFRICAN BOTANY

This Journal provides a medium for the publication of the results of botanical research primarily on the flora of Southern Africa, whether systematic, morphological, ecological or otherwise and whether carried out in South Africa or elsewhere. Papers on botanical subjects of special interest and application in South Africa may be included.

Contributions must be original and should not be translations of previously published papers.

Papers must be submitted in final, corrected form. They are accepted for publication on the recommendation of the Editorial Committee.

Authors may be charged expenses for corrections if alterations are excessive.

COPY

Papers should be type-written, double spaced throughout on one side of the paper and with margins of at least 3 cm (1 inch). Footnotes and elaborate tables should be avoided. Latin binomials should be underlined once to indicate italics. All other marking of copy should be left to the Editor. The original, plus at least one carbon copy, must be submitted.

GENERAL LAY-OUT

Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION, CONCLUSION, ACKNOWLEDGMENTS, etc.

Tables and **illustrations** should be on separate sheets. **Figures** and **graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm × 12 cm (7" × 4½"). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

TAXONOMIC PAPERS

Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations** and **herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

arranged chronologically by basionyms. Whenever possible, the types of the basionyms should be cited, e.g.:

Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. 1960: 307 (1960).

Chrysophyllum magalismontanum Sond. in Linnaea 23: 72 (1850). Type: Magaliesberg, Zeyher, 1849 (S, holo.; BOL!, SAM!).

Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

Pouteria magalismontana (Sond.) A. Meeuse in Bothalia 7: 335 (1960).

Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. 3: 641 (1898). Syntypes: Angola, Welwitsch 4827, 4828, 4829 (BM!).

Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal Wilms 1812 (B†, holo.; K!).

Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

CITATION OF SPECIMENS

In the interests of uniformity contributors are requested to follow the recommendations of the Botanical Research Institute, Pretoria (Technical note: Gen. 4, Oct., 1967) by citing specimens according to the one degree grid system. Distribution data are given separately for each province and are arranged in the following sequences: South West Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Cape. Within each province degree squares are listed in numerical sequence, i.e., from west to east and from north to south. Whenever possible locality records should be given to within a quarter degree square. The collectors' names and numbers are underlined (printed in italics) to avoid confusion with the numbers of the degree squares, e.g.: NATAL-2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Killick* 5127 (PRE); . . . CAPE-3418 (Simonstown): Hottentots Holland mountains, Somerset Sneeukop (-BB), Nov., *Stokoe s.n.* sub. SAM 56390 (SAM).

REFERENCES

These should be given in the text as follows: Jones (1968) or (Jones, 1968) or, where reference to a specific page is required, Jones (1968:57) or (Jones, 1968:57). **Literature cited** should be arranged alphabetically by surnames, chronologically within each name, with suffixes a, b, etc., to the year for more than one paper by the same author in that year. Titles of **periodicals** must be abbreviated according to the *World List of Scientific Periodicals*, 4th ed., London: Butterworth or when unable to trace the title in this list (as will be the case in taxonomic papers where abbreviations of 18th and 19th century periodicals are required) the abbreviations given in *Botanico-Periodicum-Huntianum*, Pittsburgh: Hune Botanical Library, 1968, should be followed. Periodical titles should be underlined once (for italics). If an author is unable to determine the correct abbreviation of a journal title he is advised to type it out in full and leave its abbreviation to the Editor. Titles of **books** should be underlined and given in full, together with the place of publication, name of the publisher and an indication of the edition if other than the first; e.g.:

Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy*. Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia*. *Jl S. Afr. Bot.* 26: 139-148.

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A GUIDE TO THE LITERATURE ON SOUTH AFRICAN MARINE ALGAE

S. C. SEAGRIEF AND S. C. TROUGHTON

(*Department of Botany and Microbiology, Rhodes University, Grahamstown.*)

ABSTRACT

An author list of references on the taxonomy, morphology and ecology of South African green, brown and red marine algae has been compiled.

UITTREKSEL

'N GIDS TOT DIE SUID-AFRIKAANSE SEEWIER LITERATUUR. 'n Outeurslys van verwysings oor die taxonomie, morfologie en ekologie van Suid-Afrikaanse groen-, bruin- en rooisseewiere is saamgestel.

INTRODUCTION

South African marine algae have often first been described in other countries. Also, some of the South African species which occur in other countries were described first for that country and have subsequently been found on South African shores. The references to the species are, therefore, widely scattered through the world's algological literature, dating back as far as Linnaeus in 1753.

The aim has been to compile an author list of references on the taxonomy, morphology and ecology of South African green, brown and red marine algae. Papers on physiological topics have been excluded. References to species which are at present "doubtful" records for South Africa have been omitted.

The style followed is taken from major contemporary works in Phycology. Most of the journal abbreviations are those of the *World List of Scientific Periodicals*.

Any worker, who has published mainly on South African algae, has had all his papers listed (e.g. W. E. Isaac). The compilers have examined the references in their personal possession and those in the extensive reprint collection belonging to Dr. M. A. Pocock. References not available in Grahamstown have been marked by an asterisk (*). The terminal date for entries in this guide is December, 1970.

It has not always been possible to complete the bibliographical data of the items in this list. In a few instances, where the title of the work has not yet been ascertained, the names of the species concerned are quoted in square

brackets [] to give some idea of content. It would be much appreciated if readers could assist us by sending any additional information or corrections.

Miss S. C. Troughton was formerly on the staff of the herbarium of the Albany Museum, Grahamstown where she worked under Dr. M. A. Pocock. She submitted part of this bibliography as an assignment in partial fulfilment of the requirements for the Diploma in Librarianship, Rhodes University.

Most grateful acknowledgement is made by S. C. Seagrief to the Council for Scientific and Industrial Research, for a research bursary and a travel grant to the University of California, Berkeley, where this project was initiated. It is also a pleasure to thank Professor G. F. Papenfuss and Dr. P. C. Silva, of the University of California, for their help.

We are most grateful to Dr. M. A. Pocock for giving us access to her algological literature which is housed in the Albany Museum, Grahamstown.

Finally, the authors express their thanks to Mrs. A. T. Henry, Miss A. C. Dick and Mr. R. Musiker, of Rhodes University Library, for all their assistance.

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NOTE ON *ROMULEA PARVIFLORA* ECKLON

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In his recent paper Nordenstam (1972) states that *Romulea parviflora* Ecklon may be regarded as validly published, on the assumption that Ecklon's brief note accompanying this name in the "Topographisches Verzeichniss" (1827), namely "Blume rosenroth klein", is a sufficiently clear diagnosis to warrant this view. On the other hand, in a recent revision of the South African romuleas, I regard this as a nomen nudum, Ecklon's brief note in my opinion being insufficient to validate the name, as Ecklon also "described" three more species of *Romulea*, namely *R. hirsuta* Eckl., *R. ramosa* Eckl., and *R. rosea* (Vahl) Eckl., with only the words "Blumen rosenroth". Nordenstam correctly regards the first two of these names as nomina nuda.

The view that *R. parviflora* is validly published is therefore based on Ecklon having added the word "klein" to his descriptive note "Blumen rosenroth", for *R. parviflora*—and on the discovery of Ecklon's type of the name in the herbarium of the Swedish Natural History Museum (S).

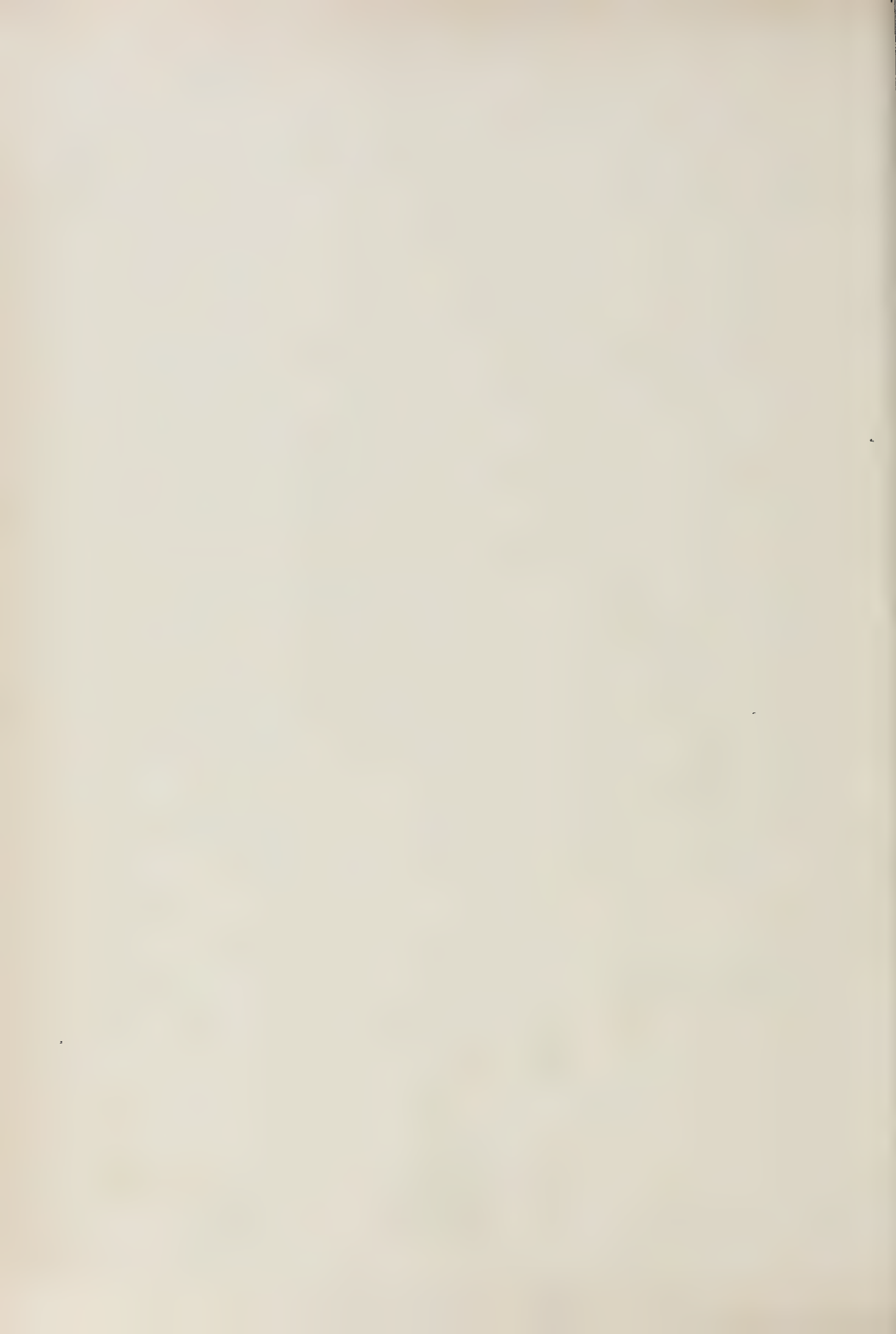
To my mind the addition of this word is not sufficient to validate the name, even if it perhaps distinguished it from other taxa in Ecklon's opinion at that time (footnote to Art. 32 of the International Code, 1972), especially as Ecklon or someone else shortly afterwards identified more specimens of *Romulea* as *R. parviflora* which are not the same as the type.

I therefore maintain that the addition of the word "klein" to the general diagnosis for three other species of *Romulea* is not sufficient reason to validate *R. parviflora*. As the type of *R. parviflora* in S is *R. obscura* Klatt, this is the valid name and *R. parviflora* goes into synonymy as nomen nudum.

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'N EMBRIOLOGIESE ONDERSOEK VAN *ROMULEA ROSEA* ECKL. VAR. *REFLEXA* BEG.*

1. Die bou, ontwikkeling en bevrugting van die saadknop.

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UITTREKSEL

Die anatropiese saadknop van *Romulea rosea* var. *reflexa* het 'n meerlagige buite-integument wat nie deelneem aan die vorming van die mikropielkanaal nie. Lg. word slegs deur die binne-integument gevorm. Aan die basis van die funiculus kom 'n klein obturator voor.

'n Primêre pariëtale sel word van die subepidermale archesporiumsel afgesny, maar in die volwasse saadknop is geen nucellus aanwesig nie. 'n Liniêre makrospoortetrade ontstaan en die chalazale een ontwikkel tot die monospore, agtkernige embriosak.

'n Klein hipostase kom voor en die groot antipodes word gedra op 'n nucelluspilaartjie. Die sinergiede het lang nekke met 'n duidelike Fadenapparaat.

Bevrugting van die eiersel is waargeneem.

Die embriologiese kenmerke van *R. rosea* word vergelyk met die van twee Suid-Europese spesies, nl. *R. bulbocodium* en *R. columnae*.

ABSTRACT

THE EMBRYOLOGY OF *ROMULEA ROSEA* ECKL. VAR. *REFLEXA* BEG. 1. THE STRUCTURE, DEVELOPMENT AND FERTILISATION OF THE OVULE. The anatropous ovule of *Romulea rosea* var. *reflexa* has a many-layered outer integument which does not contribute to the micropylar canal. The latter is formed by the two-layered inner integument only. At the base of the funiculus is a small obturator.

A parietal cell is cut off, but the mature ovule has no nucellar cap. A linear tetrad of megaspores develops of which the chalazal one becomes the monosporic eight-nucleate embryo sac.

A small hypostase is present and the well-developed antipodals are supported by a nucellar columella. The synergids have long necks in which a *Fadenapparaat* can be distinguished.

Fertilisation of the ovule could be studied.

The embryological characteristics of *R. rosea* are compared with those of two South European species, viz. *R. bulbocodium* and *R. columnae*.

INLEIDING

Romulea Maratti is 'n soortryke genus van die Iridaceae met 61 soorte in Suid-Afrika (Phillips, 1951) en word hoofsaaklik in Wes-Kaapland aangetref waar hulle as „knikkertjies” in die volksmond bekend staan. *R. rosea* Eckl. var. *reflexa* Beg. kom as 'n pionier in uitgetrapte veld, op grasperke en langs sypaadjies voor. Die klein ligpers, stervormige blommetjies verskyn in die

* 'n Verkorte weergawe van 'n deel van 'n verhandeling goedgekeur vir die graad Magister in die Natuurwetenskappe aan die Universiteit van Stellenbosch.

lente en word styf teenaan die grondoppervlak gedra tussen die lang, silindriese, unifasiale blare.

Die embriologie van *Romulea* was tot dusver feitlik onbekend, behalwe vir die werk van Ferraris (1902) en Béguinot (1907) wat die saadknoppe van twee Suid-Europese *Romulea*-soorte ondersoek het. Beide se bevindings is in nage-noeg ontoeganklike Italiaanse tydskrifte gepubliseer en het derhalwe nie die regmatige aandag van latere embrioloë wat die Iridaceae ondersoek het, geniet nie.

Ten einde die embriologie van 'n Suid-Afrikaanse *Romulea*-spesies wat volgens die knolkenmerke gevorderd is (Lewis, 1954 en De Vos, 1965) te vergelyk met die van die reeds ondersoekte, primitiewer Suid-Europese spesies, is 'n gedetailleerde embriologiese ondersoek uitgevoer op *R. rosea* var. *reflexa*.

MATERIAAL EN METODES

Jong blomknoppe, oop en ouer blomme, vrugte en sade van *Romulea rosea* var. *reflexa* is in F.A.A. gefikseer. Omdat die kutikulalae van die saadknop gedurende saadvorming verdik, is ouer saadknoppe uitgedissekteer en die saadhuide beskadig voor fiksering. Nadat die materiaal in paraffienwas ingebed is, is mikrotoomsneë van wisselende diktes na gelang die ouderdom en aard van die materiaal gemaak.

Heidenhain se hematoksilien en anilienblou het die beste resultate vir saadknopkleuring gelever. Vaughan (1955) se metode is gebruik met pikriensuur in plaas van ysteraluinoplossing.

Alle tekeninge is gemaak met 'n Zeiss-Promartekenapparaat of 'n Wild-tekenbuis.

ONDERSOEK

Posisie en vorm van die saadknop.

Die onderstandige, driehokkige vrugbeginsel van *Romulea rosea* var. *reflexa* bevat twee rye asstandige, anatropse saadknoppe in elke vrughok. Die rafe van die saadknop is dik (in die volwasse saadknop is die rafe ongeveer 100 μ m in deursnee) en bevat die vaatbondel wat in die chalaza naby die basis van die embriosak eindig.

Aanvanklik is die saadknop halfgebuig en die buiging tot die anatropse posisie vind plaas gedurende makrosporogenese in die distale deel van die funiculus. 'n Effense buiging van die integumente en nucellus kan ook waargeneem word (fig. 3).

Aan die basis van die funiculus aan die kant van die mikropiel kom 'n klein oburator voor (fig. 8).

ONTWIKKELING VAN DIE SAADKNOP

Die obturator

Die klein obturator begin ontwikkel uit 'n aantal funiculêre epidermisselle wanneer die funksionerende chalazale makrospoor begin vergroot (fig. 3). Die selle is palissadeagtig, dunwandig en sitoplasmaryk. Na 'n aantal antiklinale delings ontstaan 'n uitstulping van 'n eenlagige groepie dig opmekaargeleë selle (fig. 8). Lg. vergroot tot met antese wanneer elke sel ongeveer $29\text{ }\mu\text{m}$ lank en $8,5\text{ }\mu\text{m}$ breed is aan die seltop, maar smaller aan die selbasis.

Voor of met bevrugting verleng die palissade-agtige selle om 'n massa lang, dunwandige gekronkelde buise te vorm waarvan sommige afgeroei in die mikropielkanaal. Skynbaar dien hierdie weefsel as 'n brug vir die stuifmeelbuis (Maheshwari, 1950). In saadknoppe wat nie bevrug is nie, het die palissadeagtige weefsel nie verder ontwikkel nie.

Die nucellus

Die nucelli ontwikkel as knopvormige, meristematiese uitstulpings op die omgevoorde rande van die vrugblare. Dan het die aangrensende vrugblare reeds lateraal vergroei tot tussenskotte, maar die sentrale as van die vrugbeginsel is nog nie gevorm nie. Die nucellus groei tot 'n kort-silindriese struktuur, terwyl die integumente aangelê word (figs. 3 en 4).

Gedurende die ontwikkeling van die archesporium en makrospore bevat die saadknop 'n klein nucelluskap wat bestaan uit die nucellus-epidermis en sy derivate sowel as uit die derivate van die primêre pariëtale sel (fig. 4). Die nucelluskap bestaan uit groot, dunwandige, setmeelryke selle.

Onderkant en aangrensend aan die chalazale makrospoor is 'n paar verlengde, sitoplasmaryke nucellusselle (fig. 4) wat later dwars deel (figs. 5 en 6). Die selwande verdik (figs. 7 en 9) en verhout later, sodat die onderste helfte van die jong embriosak omgewe word deur verhoue selwande. Hierdie verhoue nucellusweefsel vorm 'n klein hipostase wat die afwaartse verlenging van die embriosak en die vernietiging van die dunwandige chalazale nucellusweefsel verhoed.

Die jong embriosak vergroot eers na die mikropilêre kant en die dunwandige nucelluskapweefsel word daardeur vernietig. Later vergroot die embriosak ook na die kante tot teenaan die binne-integument en brei dan na onder uit rondom die hipostase. Lg. bly as 'n pilaartjie oor in die wye basis van die embriosak (figs. 7 en 9) met die oorspronklike nou embriosakonderpunt as 'n keëlvormige instulping in die top van die hipostasepilaartjie.

Die volwasse embriosak is dus tenuinucellaat en die embriosakwand word van die binne-integument geskei slegs deur die oorgeblewe nucelluskutikula.

Die integumente

Die binne-integument ontwikkel as 'n kragie rondom die basis van die nucellus wanneer die archesporium verdeel (fig. 2). Effens later word die buite-

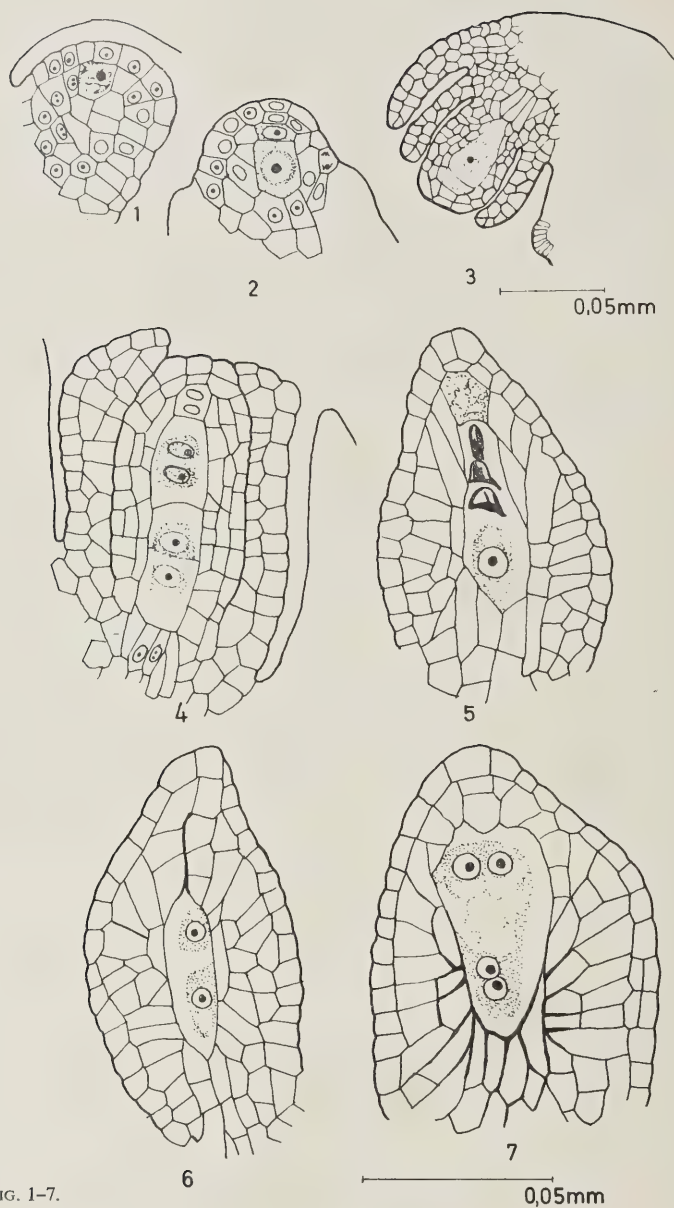


FIG. 1-7.

integument aangelê, maar is in 'n lengtedeursnee van die saadknop net sigbaar aan die teenoorgestelde kant van die rafe. Beide integumente verleng vinnig om die groeiende nucellus te bedek (fig. 3). Voordat makrosporangiese plaasvind, is die binne-integument ongeveer so lank soos die nucellus en bestaan dit uit twee sellae. Die buite-integument is effens korter as die binnenste, is drielagig aan die basis en ontbreek aan die kant van die rafe (fig. 3).

Die binne-integument vorm met verdere groei alleen die mikropielkanaal. Hierdie integument bestaan uit twee lae sitoplasmarijke, reëlmatige selle, d.w.s. slegs uit die twee epidermislae, behalwe in die mikropielkanaalstreek waar die integument verdik deurdat die buite-epidermisselle in verskeie rigtings deel. Wanneer die saadknop volwasse is, het die buite-epidermisselle onreëlmatig-verdikte gekutiniseerde wande, veral teenoor die verdwene nucelluskap en teenaan die mikropielkanaal.

Die buite-integument van die volwasse saadknop lê styf teenaan en is effens korter as die binnenste (fig. 8). In die mikropielkanaalstreek bestaan die integument uit minstens agt lae onreëlmatige, dunwandige selle, uitgesonderd die buite-epidermis. Lg. het reëlmatige donker, dikwandige, gekutiniseerde selle. Teenoor die embriosak is die buite-integument dunner.

Die archesporium en embriosak

Nog voordat die vrugblare volledig vergroei het om die sentrale as van die vrugbeginsel te vorm en voordat die integumente aangelê word, differensieer 'n subepidermale, nucellus tot die archesporium (fig. 1). Hierdie sel verdeel wanneer die binne-integument aangelê word in die primêre pariëtale sel en die primêre sporogene sel (fig. 2). Die klein plat primêre pariëtale sel aan die buitekant vergroot en verdeel later meestal om deel van die nucelluskapweefsel te vorm.

Die primêre sporogene sel wat direk as makrospoormoedersel funksioneer, vergroot tot dit aan die begin van meiose meer as die helfte van die nucelluslengte beslaan (fig. 2).

Gedurende meiose word 'n liniêre makrospoortetrad gevorm (fig. 4). Die boonste twee makrospore is kleiner as die onderste twee en word in sommige gevalle nie deur selwande geskei nie (fig. 4). Die chalazale makrospoor funksioneer en verdruk die ander drie tot struktuurlose, kappievormige selreste

FIGS. 1-7.

Lengtesnee deur die ontwikkelende saadknop van *R. rosea* var. *reflexa*: Fig. 1, jong nucellus met vergrotende subepidermale archesporiumsel; Fig. 2, jong nucellus met binne-integumentanlage, primêre sporogene sel en primêre pariëtale sel onder 'n tweelagige nucellusepidermis; Fig. 3, jong saadknop met verlengende integumente en vergrote makrospoormoedersel net voor meiose; Fig. 4, verdelende pariëtale sel en vormende makrospoortetrad; Fig. 5, funksionerende makrospoor wat die ander makrospore verdruk; Fig. 6, tweekernige embriosak geleë onder die nucelluskap; Fig. 7, vierkernige embriosak wat die mikropilêre nucellus vernietig terwyl die selwande van die chalazale nucellusselle verdik.

(fig. 5). Wanneer die aangrensende nucellusselle begin strek, word die reste lateraal platgedruk en verdwyn bokant die tweekernige embriosak (fig. 6).

In *R. rosea* var. *reflexa* word die mikropilêre en chalazale kwartetkerne gelyktydig gevorm. Die boonste vier kerne lê in die sitoplasmalaag van die wye embriosakbopunt en die onderste vier kerne in die nou onderpunt. Dikwels kan slegs sewe kerne onderskei word, omdat die twee poolkerne baie gou versmelt. Die sekondêre embriosakkern lê dan net bo die antipodekerne. As die embriosak nog relatief klein is, is die sekondêre embriosakkern verbind met die eierkern d.m.v. 'n aksiale sitoplasmastring, maar in die volwasse embriosak is hierdie verbinding moeilik om vas te stel.

Die sekondêre embriosakkern is rond of effens afgeplat aan die chalazale kant en ongeveer $20\text{ }\mu\text{m}$ in deursnee, met 'n opvallende groot nukleolus, yl chromatiennetwerk en 'n dun kernmembraan.

Die drie antipodes differensieer voor die eierselapparaatelemente, as omgekeerd-peervormige selle in die nou embriosakonderpunt. Namate die embriosak vergroot, stulp die bolvormige deel van die selle uit die embriosakonderpunt na bo. Die volwasse selle wat ongeveer $60\text{ }\mu\text{m}$ lank is en 'n maksimum deursnee van $43\text{ }\mu\text{m}$ het, word dus op die pilaarvormige hipostase gedra (fig. 9).

Die sinergiede is peervormige, styfteenmekkaarliggende selle met lang, smal nekke wat deur die nucelluskutikula dring en tot aan die basis van die mikropielkanaal strek. Die sitoplasma is gekonsentreerd in die nek en rondom die kern wat in die middel van die sel teenaan die buitewand lê (fig. 10). Met antese is die sinergiede ongeveer $72\text{ }\mu\text{m}$ lank. Die $40\text{ }\mu\text{m}$ lang nekke bevat die sg. Fadenapparat wat helderblou met anilienblou kleur en die aanwesigheid van kallose suggereer.

Die eiersel is rond tot ovaalvormig en lê in die middel van, styf teenaan en effens laer as die twee sinergiede. Die kern en die meeste sitoplasma lê in 'n halfmaanvormige laag in die onderste selgedeelte (fig. 10). Met antese is die eiersel meestal $28 \times 20\text{ }\mu\text{m}$ groot.

BEVRUGTING

In *R. rosea* var. *reflexa* dring waarskynlik net een stuifmeelbuis die saadknop deur die mikropiel binne. Slegs in een bevrugte saadknop is 'n tweede, onbeskadigde buis met 'n opgeswelde punt in die mikropielkanaal gekry.

Gedurende bevrugting word een sinergied deur die stuifmeelbuis vernietig. Na bevrugting is die oorblyfsels van die nek gewoonlik nog herkenbaar. Die ander sinergied bly behoue en gaan eers tot niet nadat die embrio die kwadrantstadium bereik het.

FIGS. 8-11.

Mediane lentesneë deur die saadknop van *R. rosea* var. *reflexa*: Fig. 8, die saadknop net voor bevrugting; Fig. 9, die antipodes en sekondêre embriosakkern gedra op die nucelluspilaartjie; Fig. 10, die sinergiede en eiersel; Fig. 11, bevrugting van die eiersel: ob, obturator; ei, eierselkern; gen, spermkern; stb, stuifmeelbuis.

Met bevrugting dring een manlike gameet die eiersel binne en die ronde spermkern lê dan langs die eierkern (fig. 11). Die eierselkern behou sy vorm, maar die spermkern raak afgeplat, lê styf teen die eierkernwand en verdwyn langsamerhand. Die nukleolus is in die laaste stadia van versmelting nog sigbaar buitekant die eierkernwand. Die bevrugte eierkern bevat twee nukleoli waarvan die een, afkomstig van die spermkern, kleiner is as dié van die eiersel.

Die versmelting van die tweede manlike gameet is nie gesien nie. Die eerste endospermkerne is kleiner as die sekondêre embriosakkern en lê in die aksiale sitoplasmastring wat die eierapparaat met die antipodes verbind, of in die wandstandige sitoplasma naby die antipodes se basisse. Gewoonlik het die endospermkerne 'n groot en 'n klein nukleolus en in enkele gevalle is drie nukleoli opgemerk.

Gedurende bevrugting en die aanvangstadia van endospermvorming is al drie antipodes nog aanwesig, maar hulle verdwyn voordat die sigoot begin deel.

BESPREKING

Die huidige ondersoek toon die noue verwantskap tussen *R. rosea* var. *reflexa* van die Suidwestelike Kaap en *R. columnae* en *R. bulbocodium* van Suid-Europa. Nieteenstaande hulle geografies deur duisende myle, waarskynlik vanaf prehistoriese tye van mekaar geskei is, is die embriologiese verskille tussen die spesies, soos hieronder aangetoon word, gering.

1. Die saadknop van *R. rosea* var. het aan die basis van die funiculus 'n klein obturator wat afwesig is by die Suid-Europese soorte.
2. By *R. rosea* var. is die buite-integument van die saadknop dikker as die binne-integument, maar korter, sodat 1g. alleen die mikropielkanaal vorm. Volgens Béguinot is beide integumente by die Suid-Europese soorte tweelagig. Die buite-integument is langer as die binnenste en vorm 'n eksostomium (Ferraris, 1902).
3. By *R. rosea* var. word gedurende meiose vier makrospore gevorm waarvan die boonste twee in sommige gevalle nie deur 'n selwand van mekaar geskei word nie. Volgens Ferraris (1902) word net drie makrospore in bg. twee *Romulea*-soorte gevorm. Die boonste diadesel verdeel nie, maar word vroeg plat gedruk.
4. Die agt kerne van die embriosak word by *R. rosea* var. gelyktydig gevorm, maar in die ondersoekte Suid-Europese soorte is die vorming van die mikropilêre kernkwartet vertraag. Wanneer daar reeds vier kerne in die embriosakonderpunt is, deel die mikropilêre kern vir die eerste keer (Ferraris, 1902).
5. Die twee poolkerne in die agtkernige embriosak versmelt by *R. rosea* var. so gou dat daar gewoonlik net sewe kerne sigbaar is en die sekondêre embriosakkern het dan net een groot nukleolus. By *R. bulbocodium* en *R.*

columnae bly die twee poolkerne vir 'n tyd lank onderskeibaar en die twee nukleoli van die sekondêre embriosakkern versmelt eers later.

6. Die sinergie bly by *R. rosea* var. langer sigbaar na bevrugting en is $72\ \mu\text{m}$ lank, vergeleke met $43\ \mu\text{m}$ by die Suid-Europese soorte, maar strek nie op in die mikropilumkanaal soos Béguinot (1907) beweer nie.

R. bulbocodium en *R. columnae* word weens sekere uitwendig-morfologiese kenmerke as primitief beskou, terwyl *R. rosea* meer gevorderd is (De Vos, 1968, persoonlike mededeling). Hier bied die embriologie geen bykomende getuienis nie, soos uit bg. klein verskille blyk, omdat embriologiese kenmerke waarskynlik meer konstant is as uitwendig-morfologiese kenmerke.

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MYCORRHIZA IN CERTAIN ERICACEAE NATIVE TO SOUTHERN AFRICA

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ABSTRACT

The roots of selected species of *Erica* growing under natural conditions and in cultivation were examined to assess whether or not mycorrhizal associations were present. Infection was recorded in every case. The fungi necessary to bring about mycorrhizal formation are, therefore, of widespread occurrence in South African soils, and no specific host/fungus relationships appear to exist.

UITTREKSEL

MYCORRHIZA IN SEKERE SUID-AFRIKAANSE ERICACEAE. Die wortels van uitgesoekte spesies van ERIKA, wat onder normale omstandighede gegroei asook gekweek is, is ondersoek ten einde vas te stel of mycorrhizal verbindings teenwoordig is of nie. Besmetting is in elke geval gevind. Die fungus wat mycorrhizal formasies veroorsaak kom dus wyd verspreid in Suid-Afrikaanse grond voor en geen spesifieke gasheer/fungus verhouding blyk te bestaan nie.

INTRODUCTION

Most of the families in the Ericales have been reported as including genera which are mycorrhizal, and the Ericaceae, in particular, are prone to this form of infection (Harley, 1969). The roots of this family are typically fine in structure, and, under natural conditions, many of them are surrounded by a loose web of hyphae, which, in addition, may penetrate the cells of the cortex. Within these outer cells the hyphae proliferate to form compact 'clumps', but after a period of 'maturity' the hyphae are digested by the host cell. The balance between infection and digestion appears to depend on the vigour of the host, and hence the degree of infection will vary with growing season.

The fact that *Erica* spp. growing under natural conditions are infected in this manner has been interpreted as indicating that the presence of the fungus is essential for development of the host. (Rayner, 1925). The nature of the advantage derived by the host from the association is open to speculation, but, if the hypothesis is valid, then one would expect all species of heath to be infected. In addition, if a close relationship exists between host and fungus, it is possible that some degree of host specificity will exist among potential mycorrhizal fungi. If this were so, then the relatively local distribution of some heaths in South Africa might be explained, in part, by the absence of a suitable

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endophyte outside a specific geographical range. It is also possible that such specificity would raise problems for growers attempting to cultivate species for the consumer market.

It was decided to examine this question in relation to certain heaths in three ways:

- (a) by examining root material of a number of *Ericas* both from natural locations and cultivated sites in South Africa;
- (b) to grow a range of species from seed on soils known to have not recently supported an Ericaceous host, and to determine whether the roots of these plants become mycorrhizal;
- (c) to isolate the endophytes from a number of South African heaths, and to test, under aseptic conditions, whether a particular isolate could produce normal mycorrhizal associations with test seedlings of other *Erica* spp.

MATERIALS AND METHODS

Twelve species of *Erica* were selected, and root material was collected from specimens growing under natural conditions (see Table I). Roots were collected for examination by removing a core of soil, 1 in. $\times$ 6 in. (2.5 cm $\times$ 15.3 cm), from beside a selected plant. Three cores were obtained for each species. The material was soaked in water overnight to loosen the fine roots; these were then removed with forceps. Subsequently the roots from the three plants were bulked; one half of the sample was placed in fixative (formalin/acetic acid/ethanol (50%); 1:1:18), the other half was kept in distilled water at 5°C for a maximum of 24 hours prior to isolating the endophyte.

A similar procedure was followed for obtaining roots from equivalent specimens in cultivation in South Africa.

In the case of those species which were to be grown under experimental conditions, seed was obtained from the National Botanic Garden at Kirstenbosch. The seed was pre-germinated on moist, sterilized peat, and twelve seedlings were transferred to 6 in. (15.3 cm) pots containing a locally obtained acid soil (pH 4.2). The most vigorous seedlings were selected until only one plant remained in each pot. Six pots were planted for each species. The selected plants were maintained in the greenhouse with a mean air temperature of 16°C for twelve months.

The fine nature of the roots makes handling of individual specimens difficult, and accordingly small groups attached to a fine lateral root were embedded and sectioned (Johansen, 1940). The sections were stained in alcoholic chromotrope 2R (saturated soln.) for two hours. Clear differentiation of the endophyte within the cortical cells was obtained in this way.

The isolation of the endophytes was carried out using the technique of Bain (1937). A pure culture from each species of *Erica* was maintained on

potato-dextrose agar for experimental purposes; only isolates from non-cultivated hosts were subsequently used.

To examine whether any host/fungus specificity existed, seed of the six species grown previously (see Table I) was surface sterilised with 10% calcium hypochlorite for 10 minutes: after washing in sterile distilled water, six seeds were transferred to the surface of agar slopes in test-tubes (2 cm diam.). The medium was 1% distilled water agar, as the use of this substrate avoids problems of nutrient toxicity, (Bain, 1937). This system was chosen to reduce the risk of extraneous infection (Brook, 1952), and in practice it was found that seedlings grown under these conditions for twelve weeks were comparable to soil-grown plants of the same age. The tubes, half-covered with black paper, were then placed in racks on a bench in a greenhouse (16°C). After one month the developing seedlings were inoculated by placing two inoculum discs (3 mm) of agar plus mycelium onto the surface of the water agar. The design used for carrying out the inoculations is shown in Table II. Ten tubes of each species of *Erica* were inoculated with each of the six available fungi. After two months the seedlings were removed and examined for mycorrhizal infection in the manner described previously.

RESULTS

The species examined for the presence of mycorrhizal infection are shown in Table 1.

TABLE I
Origin of *Erica* spp. used in the current investigation.

Species	Origin	
	'Wild'	Cultivated
<i>Erica blenna</i> , Salisb.	Cape Province	Pretoria*
<i>E. baueri</i> , Andre	Cape Province	Pretoria
<i>E. oatesii</i> , Rolfe	Transvaal	Pretoria
<i>E. inflata</i> , Thunb.	Cape Province	Pot grown
<i>E. ventricosa</i>	Cape Province	Pot grown
<i>E. daphniflora</i> , Salisb.	Cape Province	Pot grown
<i>E. lateralis</i> , Willd.	Cape Province	Pot grown
<i>E. mammosa</i> L.	Cape Province	Pot grown
<i>E. sessiliflora</i> L.	Cape Province	Pot grown
<i>E. campanularis</i> , Salisb.	Cape Province	Pretoria
<i>E. cerinthoides</i> L.	Cape Province	Pretoria
<i>E. regia</i> Bartl.	Cape Province	Cape Town†

* Gardens of the Botanical Research Institute.

† National Botanic Gardens, Kirstenbosch.

(Nomenclature follows Baker and Oliver, 1967).

A number of root samples from each species were examined, and in every case cortical cells showing the type of mycorrhizal infection normally associated with the Ericaceae were found. No attempt was made to assess the degree of infection displayed by a particular species, but two examples of the type of infection are shown in Plate: I. The frequency of infection suggests that the fungi capable of forming mycorrhizal associations with *Erica* spp. are present in a wide range of soils.

The fungi responsible for the endotrophic associations in the *Erica* spp. examined were basically similar in appearance, although some variation with respect to pigmentation was recorded. The colonies were composed of septate hyphae without clamp connections, and (when young) varied in colour from pale to dark grey. With age, the central region of the colony tended to become almost black, and, with some isolates, semi-stromatic. The depth of colouration depended, in part, on the medium and was not a constant characteristic for

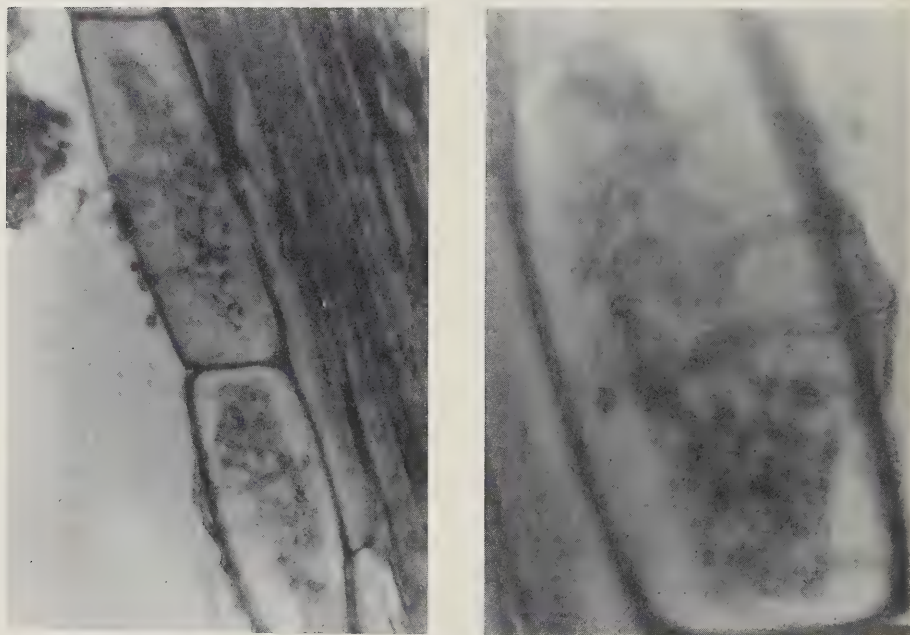


PLATE I

Roots of *Erica lateralis* showing typical mycorrhizal infection: (right x 1000) showing 'clump' of invading hyphae:

(left x 400) showing surface mycelium and penetration of the individual cells.

any particular isolate. The complete absence of fruiting structures meant that no exact systematic position could be established, although Booth (personal communication) tentatively identified an isolate from *Erica lateralis* as a species of *Hypoxylon* (Xylariaceae).

However, despite the apparent morphological similarity of the cultures examined, the variable degree of melanisation, for example, suggested that physiological differences might exist between isolates. Such variation might manifest itself also in relation to host specificity, and this idea was examined by testing the virulence of a particular fungus towards the *Erica* sp. from which it had been isolated, as well as towards species with which it had not had immediate contact. The results are shown in Table 2.

TABLE 2

Mean number of plants of *Erica* spp. showing mycorrhizal infection after being inoculated with the endophyte from another host.

Endophyte isolated from:	Test seedlings of:					
	<i>Erica inflata</i>	<i>E. ventricosa</i>	<i>E. daphniflora</i>	<i>E. lateralis</i>	<i>E. mammosa</i>	<i>E. sessiliflora</i>
<i>Erica inflata</i>	6	3	2	5	5	2
<i>E. ventricosa</i>	3	2	1	5	3	3
<i>E. daphniflora</i>	3	1	2	6	1	3
<i>E. lateralis</i>	5	2	2	4	2	1
<i>E. mammosa</i>	5	1	1	5	3	2
<i>E. sessiliflora</i>	1	3	6	5	2	3

In each case the assessment was based on the mean result of five tubes selected at random from each batch. Infection was recorded only when the roots of the seedlings showed typical mycorrhiza. It is clear from Table II that no precise relationship exists between the mycorrhizal fungi and their hosts.

DISCUSSION

The present investigation confirms that infection of *Erica* spp. in South Africa is a general and widespread occurrence, and that both wild and cultivated specimens become infected without difficulty. The apparently ubiquitous distribution of these associations suggests that the Ericaceae may, through the presence of the endophyte, be at a selective advantage in competing with other plant species. Thus, in typical fynbos vegetation, *Erica* spp. have been observed

to be dominant in localised patches, and it is possible that selection is operating to form a more homogeneous community. However, such a view must remain mere speculation until it can be shown that the endophyte is materially important to the survival of the host.

It has been proposed by Morrison (1957) that the endophyte assists with nutrient absorption in the manner of the ectotrophic mycorrhizas of forest trees. However, this hypothesis lacks real experimental verification, as does the suggestion of Friesleben (1934), that the mycorrhizal fungi stimulate root growth by the removal of phytotoxic materials in the rooting medium. One last hypothesis which may merit further attention is that the mycorrhizal fungi, in conjunction with the host roots, produce fungitoxic metabolites (Robinson, 1972). These compounds might be effective, either in preventing the roots of *Erica* spp. being invaded by pathogens (Stalder & Schültz, 1957) or, by inhibiting the growth of other mycorrhizal fungi, in restricting the growth of certain plant species whose presence would be to the detriment of the Ericaceous shrubs (Handley, 1963).

However, whatever may be the true relationship between endophyte and host in *Erica* spp., it is clear that an understanding of the physiological basis of the association might go some way towards explaining the success of this genus under certain ecological conditions.

CONCLUSION

Certain species of *Erica* native of South Africa were found to have mycorrhizal infections irrespective of where they were grown. Thus, specimens in cultivation were just as heavily infected as individuals growing under natural conditions. It is clear, therefore, that the endophyte(s) enjoys widespread distribution, at least in acid soils, and that cultivation of *Erica* spp. either within the Republic or outside is unlikely to be hindered by the lack of a suitable mycorrhizal fungus. The precise identity of the fungal associates remains obscure, as does the real significance of the infection in relation to the host.

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TWO NEW GENERIC RECORDS OF MOSSES FOR SOUTHERN AFRICA

by

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ABSTRACT

The moss genera *Bryobartramia* and *Eccremidium* are newly recorded from South Africa, the first from the Clanwilliam division of the Cape Province and the second from the Bergville district of Natal.

UITTREKSEL

TWEE NUWE GENERIESE REKORDS VIR MOSSE IN SUID-AFRIKA. Die mosse genera *Bryobartramia* en *Eccremidium* is nog nie vantevore in Suid-Afrika gevind nie. Nou is eersgenoemde in die Clanwilliam distrik in die Kaapprovinsie en die laasgenoemde in die Bergville distrik, Natal, gevind.

As a result of the collection of small terrestrial mosses by both authors, two new generic records of mosses for South Africa have come to light. They have almost certainly escaped detection in the past because of their small size and ephemeral nature. It is interesting to note that these two genera were previously regarded as Australian endemics. Also, two recent new bryophyte records for Africa (Schelpe, 1969) were previously only known from Australasia. Yet another taxon collected near Clanwilliam appears to represent an undescribed cleistocarpous genus of the Dicranaceae.

BRYOBARTRAMIA SAINSB.

This monotypic genus is typified by *Bryobartramia robbinsii* Sainsb.* previously only recorded from "grassland or grass forest land", in Victoria, Australia. In South Africa, the species was collected by one of the authors (E.A.C.L.E.S.) on a roadside, south aspect, shale/clay slope seven miles south

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* A new combination for this species *Bryobartramia novae-valesiae* (Broth.) Stone and Scott *comb. nov.* (basionym: *Trachycarpidium novae-valesiae* Broth. ex Roth.) is in the course of publication elsewhere.

of Clanwilliam on the road to Algeria, Cape Province (5.x.1972). The associated vegetation is scrub comprising *Euclea*, *Rhus*, *Galenia*, *Elytropappus* and *Euphorbia mauritanica*.

Bryobartramia has the habit of a comparatively large *Ephemerum*, but is peculiar in that the enlarged archegonium does not split off to form a calyptra but continues growth and envelops both the seta and mature capsule. On these grounds, Sainsbury (1948) referred it to a separate family, the Bryobartramiaceae.

ECCREMIDIUM WILS.

This genus of the Dicranaceae is similar in aspect to *Pleuridium*, but has a well differentiated operculum to the capsule. Immature specimens collected by one of the authors (I.G.S.) are similar to *E. exiguum* (Hook. f. & Wils.) Wils., one of the four Australian endemic species of the genus. These specimens were found near the base of a path-side earth-bank, near the entrance to the Tugela Gorge, in the Royal Natal National Park, Bergville district, Natal (23.iii.1972). Mature specimens should be sought in April.

Specimens of these new generic records are lodged in the Bolus Herbarium, University of Cape Town (BOL).

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BIOSYSTEMATIC AND TAXONOMIC STUDIES IN *HOMERIA* (IRIDACEAE)

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ABSTRACT

Ecological, cytological and morphological data are presented in comparing two western Cape (South Africa) species of *Homeria*, *H. collina* (also known as *H. breyniana*) and *H. flaccida* (= *H. breyniana* var. *aurantiaca*). The evidence presented is used as reason for raising the rank of *H. flaccida* from varietal status to species. A brief taxonomic history of both species, explaining the nomenclatural changes, is followed by synonymy and brief descriptions.

UITTREKSEL

BIOSISTEMATIESE EN TAKSONOMIESE ONDERSOEK VAN *HOMERIA* (IRIDACEAE). Ekologiese, sitologiese en morfologiese data word aangebied waar twee Wes-Kaapse (Suid-Afrika) soorte *Homeria*, nl *H. collina* (ook bekend as *H. breyniana*) en *H. flaccida* (= *H. breyniana* var. *aurantiaca*) vergelyk word. Die getuigenis aangebied word gebruik om *H. flaccida* van varieteits rang na soort rang te verhef. 'n Kort historiese oorsig oor die taksonomiese geskiedenis van beide soorte se naamsverandering word gevolg deur 'n lys van sinonieme en kort beskrywings.

INTRODUCTION

Homeria is a common genus of the Iridaceae in many parts of South Africa and is very well represented in the winter rainfall area of the south western Cape. The genus, many species of which are known locally as tulps, comprises about 35 species all of which are herbaceous geophytes usually flowering in spring or summer. Several species have been cytologically studied (Goldblatt 1971); the basic chromosome number (x) is 6 and while most species are diploid, $2n = 12$, two tetraploids, $2n = 24$, (*H. pura* from the Transvaal and *H. collina*), and one hexaploid, $2n = 36$, (*H. flaccida*), are known. The two species dealt with in this paper have long been known to science and to local botanists, and are common within their range in the south western Cape. *Homeria flaccida* Sweet, treated since the end of the nineteenth century (Baker, 1892) as var. *aurantiaca* of *H. collina* (either as *H. collina* or as *H. breyniana*) is regarded as a distinct species in this paper. A suggestion to this effect was first made by the present author (Goldblatt 1971) based mainly on chromosomal evidence. The discovery of naturally occurring sterile hybrids in 1970 stimulated a deeper investigation of these two taxa and the author now feels fully justified in changing the rank of var. *aurantiaca* to species level.

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In reviewing the taxonomy of these species, name changes of both were found necessary. A brief resume of their taxonomic history is therefore presented following the discussion of ecology and morphology and the studies of chromosome cytology in these two species and their hybrid.

BIOSYSTEMATICS

Ecology and phenology

Homeria collina is a very early flowering species often found in full flower from May or June to early August. Late flowering plants are not uncommon and scattered individuals may be found at higher elevations even in late September. *Homeria collina* is fairly tolerant of different habitats and can be found commonly from sea level to altitudes of above 600 feet, either in clay or sand (the two major soil types in its geographic range). Morphologically it is distinct, having a comparatively large flower for the genus, but it is slender and seldom has more than one branch. The flower which may be pale pink or pale yellow, is somewhat cup-shaped at the base, with only the upper parts of the perianth spreading.

Homeria flaccida is on the other hand a late flowering species most common in early October. It shows a preference for moist situations and is usually found in seasonally inundated depressions or marshy places and never occurs at high elevations. It is a robust, usually much branched, tall and many flowered species. The flowers are large, more open than those of *H. collina* with the perianth segments spreading from the base, and they are bright orange with a yellow streak at the base of each petal. Live specimens cannot be confused with those of any other species, but much character is lost when dry. One feature, a very long ovary, is characteristic and though it is variable, it is amongst the longest of all species of *Homeria*.

*Cytology**

The chromosomes of *H. collina* were first described by Sakai (1952) who reported $2n = 24$. Subsequently the present author (Goldblatt 1971) confirmed the report for this species (under the name *H. breyniana*). *Homeria flaccida* (as *H. breyniana* var. *aurantiaca*) was described as having a diploid number of $2n = 36$, also by Goldblatt (1971). Present observations confirm these records for several populations of both species. Both yellow and pink forms of *H. collina* have a diploid number of $2n = 24$. Meiotic studies of both species reveal no unusual behaviour of the chromosomes. Both species are obligate out-crossers.

* The cytological method employed here is the same as that previously described by the author (Goldblatt 1972).

TABLE 1.

Chromosome numbers in several populations of *Homeria flaccida* and *H. collina*. Voucher specimens collected by the author are housed at the Bolus Herbarium, University of Cape Town.

Species	Diploid number	Locality
<i>H. flaccida</i>	2n = 36	Kommetjie, Cape Peninsula
	36	Mud River Farm, Darling
	36	Twenty Four Rivers, Gouda
	36	Kirstenbosch, Cape Peninsula
<i>H. collina</i>	2n = 24	Paarl, Cape
	24	Lions Head, Cape Peninsula
	24	Fish Hoek, Cape Peninsula
	24	Oudekraal, Cape Peninsula

Hybrid Studies

At one site on the Cape Peninsula hybrid plants (*H. flaccida* $\times$ *H. collina*) were found. These resemble *H. flaccida* in habit, but have flowers intermediate in size and colour between those of *H. flaccida* and those of *H. collina* and have a diploid number of $2n = 30$ (fig. 1: C). Growing amongst the hybrids were several typical plants of *H. flaccida* but no *H. collina* were found still in flower, although numerous seed-bearing plants were located nearby. The hybrids were growing in a disturbed habitat along a roadside in a thick growth of Kikuyu grass (an exotic species, *Pennisetum clandestinum* Hochst. ex Chiov.)

The hybrids were all sterile but corms transplanted to a test site produced healthy plants in following seasons. Crossing with pollen of both parent species failed to produce any seed at all.

Meiosis and microspore development

The hybrids, all with 30 somatic chromosomes, exhibited several abnormalities during meiosis, typically recorded for triploids or pentaploids. Pairing at diakinesis varied, and between 9 and 12 bivalents and between 12 and 6 univalents were found (fig. 1: A). The unpaired chromosomes usually lie on the periphery of the metaphase plate and lag during anaphase. This commonly results in their exclusion from the nuclei formed during telophase of the first division of meiosis and subsequently the second meiotic division. A tetrad of large, normal looking nuclei regularly forms, while several micronuclei may be found, presumably each containing only the single chromosomes which had failed to pair during early meiosis (fig. 1: B).

Both normal looking pollen and micro pollen grains are ultimately produced by the hybrid. The bulk of the normal sized pollen is apparently fertile and stains brightly in aniline blue. In spite of the appearance of this pollen, no fruit development or seed is ever produced using it as male parent in crosses with the hybrid or with either parent. It is clear that no gene exchange is possible between *H. flaccida* and *H. collina* through such hybrids.

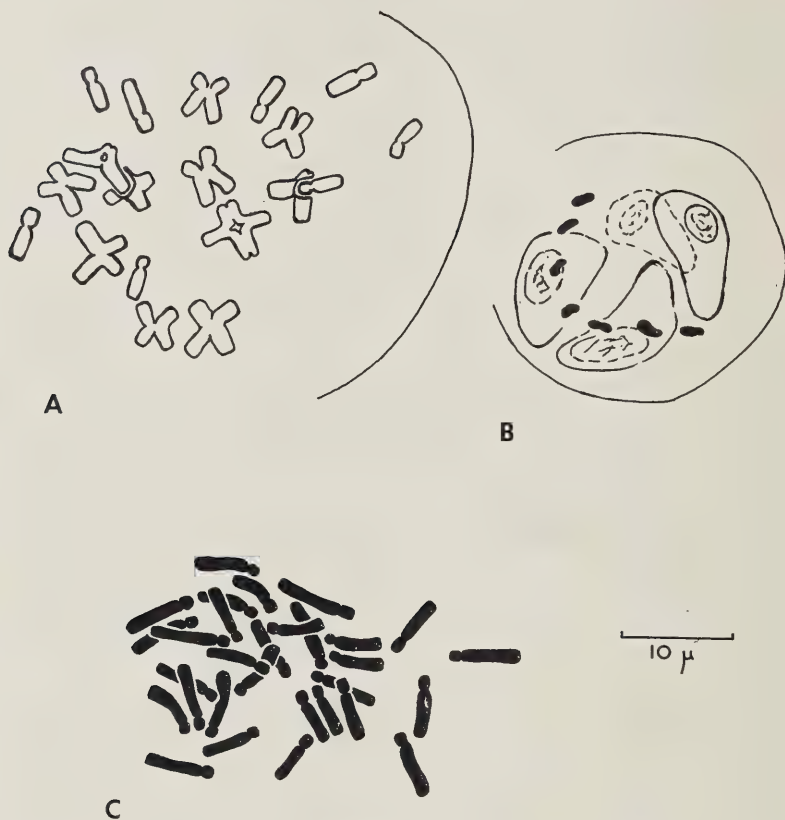


FIG. 1.

Cytology of the hybrid *Homeria flaccida* $\times$ *Homeria collina*. A. Meiotic metaphase in pollen mother cell; B. Early tetrad in microsporangium; C. Somatic mitotic metaphase, $2n = 30$ (A and C according to given scale, B half given scale.)

Though it appears that *H. collina* may be one parent of the apparently allohexaploid *H. flaccida*, simply because it is one of the few known tetraploid species of *Homeria*, and the only tetraploid within the range of *H. flaccida*, the absence of a consistent production of 12 bivalents in the hybrid *H. collina* $\times$ *H. flaccida* argues against such a simple explanation.

In the only other interspecific hybrid in *Homeria* known to the author, an artificially produced cross between *Homeria miniata* and *H. elegans*, both diploid

species, pairing was frequently normal, though in a few cases two univalents occur. Like the *H. flaccida* $\times$ *H. collina* hybrid it is totally sterile in spite of the normal meiosis in microsporangia and the production 50% normal, apparently viable pollen. The fairly constant production of six bivalents in a cross between two such unrelated species would lead one to assume that if *H. collina* were one ancestor of *H. flaccida*, then regular pairing should be expected in the *H. collina* $\times$ *H. flaccida* hybrid. It is however clear that more cytological studies are necessary in the genus, especially in hybrids, before the evolution of polyploid forms such as *H. flaccida*, or for that matter *H. collina*, can be understood.

TAXONOMY

Homeria collina (Thunb.) Vent.

This species was first described by Thunberg (1787) who recorded it as a *Moraea*. Thunberg's clear observations on its early flowering habit, its abundance and the occurrence of both yellow and pink forms on the Cape Peninsula make it easy to recognise and its identity has never presented problems. It is typified by adequate material at the Thunberg Herbarium in Uppsala.

In 1941 Lewis reduced *H. collina* to synonymy as she believed that a previously described Linnaean species *Tulipa breyniana* was conspecific. This latter species is described only from an illustration in Breyne (1678), later copied by Rudbeck (1701), of what clearly seems to be a poorly illustrated, already wilted plant possibly a *Homeria*. This picture (fig. 2) is obviously partly based on a true plant and partly on the artist's reconstruction of what he imagined the wilted specimen was, in this case a tulip, and the gynoeceum of a tulip is represented on what otherwise is probably an *Homeria*. Lewis believed this species to be the same as *H. collina*, an assumption which under the circumstances appears unwarranted. While the present author does not argue with her generic determination, it seems most unsatisfactory to attempt specific determination from the poor illustration, especially as *Homeria* is a very difficult genus in which to identify species. Apart from this it appears to the present author that *Tulipa breyniana* is closer (though this cannot be confidently stated) to other species of *Homeria*, e.g. *H. ochroleuca* or *H. comptonii* rather than to *H. collina*. The description given by Breyne does not help, and in fact, without the illustration it is impossible even to suggest the identity of his *Sisyrinchium ex phoeniceo suaverubente flore Aethiopicum*. Thus it is advisable to reject *Tulipa* (or *Homeria*) *breyniana* and revert to the name *Homeria collina*.

Homeria flaccida Sweet

This plant, named by Sweet in 1826, is based on the illustration in Curtis' Botanical Magazine t. 1612; it was renamed *H. aurantiaca* by Sweet several years later (1830) and it remained known by this epithet until Baker (1892) reduced it to varietal status under *H. collina*. Lewis (1951) continued to regard

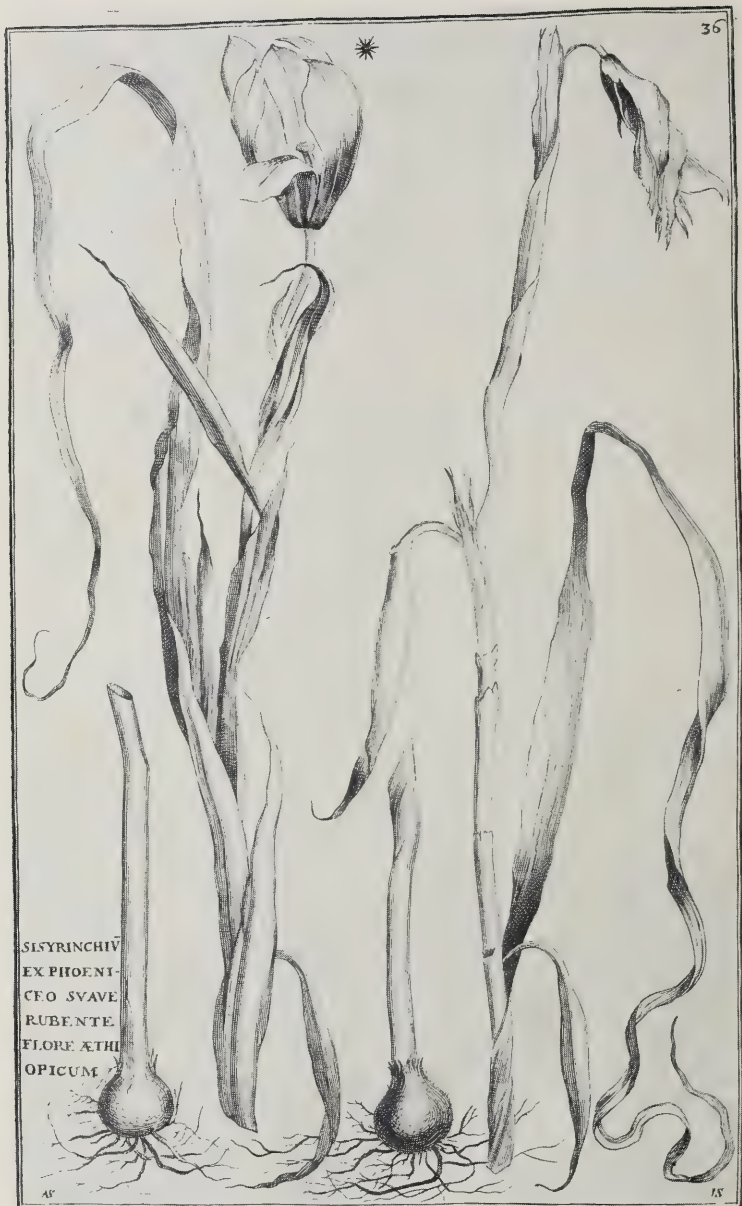


FIG. 2.

this plant as a variety of *H. collina*, as *H. breyniana* var. *aurantiaca* (Sweet) Lewis. It is raised to specific status once again, based on the ecological, morphological and cytological evidence presented in this paper.

As complete a synonymy as is currently known is presented together with brief descriptions.

1. ***Homeria collina*** (Thunb.) Vent., Decad. no. 2: 5 (1808).

Moraea collina Thunb., Diss. Moraea.: 11, no. 13 (1787).

Sisyrinchium collinum (Thunb.) Cavan.,¹ Diss. 6: 346 (1788).

Homeria breyniana sensu Lewis in Jl S. Afr. Bot. 7: 57–59 (1941) non *Tulipa breyniana* L.

Plants rarely exceeding 45 cm, slender, seldom bearing more than two branches. *Produced leaf* narrow and inserted well above ground level. *Flowers* pale yellow or salmon pink, segments fading to pale greenish yellow near base; *perianth segments* unequal, outer larger; held erect with distal parts only spreading; segments widening gradually towards apex. *Filament* column distinctly pubescent; *anthers* reaching to base of stigmas. *Ovary* 1–1.6 cm long; *capsule* rarely exceeding 3 cm.

Type: Cape Peninsula, Thunberg in Herb. Thunb. (UPS, holotype!).

Distribution: southern and south western Cape.

Flowering time: May to September.

2. ***Homeria flaccida*** Sweet, Hort. Brit. ed 1: 395 (1826), based on *H. collina* var *miniata minor* Ker in Curtis' Bot. Mag.: t. 1612 (1814).

Moraea flaccida (Sweet) Steudel, Nom. ed 2: 160 (1840).

Homeria collina var *flaccida* (Sweet) Klatt in Linnaea 34: 629 (1865).

Homeria collina var *miniata minor* Ker in Curtis' Bot. Mag. t. 1612 (1814).

Moraea aurantiaca Eckl., Top. Verz.: 15 (1827) nom. dubium.

Homeria aurantiaca Sweet, Hort. Brit. ed. 2: 498 (1830), based on *H. collina* var *miniata minor* Ker in Curtis' Bot. Mag. t. 1612 (1814).

Homeria collina var *aurantiaca* (Sweet) Bak., Handbk. Irid.: 75 (1892).

Homeria breyniana var *aurantiaca* (Sweet) Lewis. In: Adamson & Salter, Flora of the Cape Peninsula (1950).

Plants tall, robust and usually bearing several branches, reaching to 60 cm. *Produced leaf* broad and strap like, inserted near base of scape. *Flowers* bright orange red, yellow near base of segments; *perianth segments* unequal, spreading almost from base, outer segments equally wide for whole length of limb. *Filament* column barely or not pubescent; *anthers* long and usually exceeding the stigmas. *Ovary* 1.5–2.5 cm long; *capsule* long, sometimes exceeding 4 cm.

FIG. 2.

The type illustration of *Tulipa breyniana* L. which was published in Breyne, *Plantarium Exoticarum Centuria Prima* (1678).

Type: illustration in Curtis' Bot. Mag. : t. 1612 (1814).

Distribution: Cape Peninsula and north to Piketberg and Saldanha Bay.

Flowering time: September and October.

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A REAPPRAISAL OF TYPE AND AUTHENTIC SPECIMENS OF BASIDIOMYCETES IN THE VAN DER BYL HERBARIUM, STELLENBOSCH

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This paper is an account of type or authentic specimens of those species of Basidiomycetes other than Uredinales and Ustilaginales described by P. A. Van der Byl and which are preserved in his herbarium at the University of Stellenbosch, STE. However, Van der Byl was in the habit of sending material for naming to C. G. Lloyd at Cincinnati, U.S.A., who based many new species on Van der Byl's collections. In most instances duplicated material of the collections sent to Lloyd are preserved in the Van der Byl herbarium and these too have been studied and described in this paper. It sometimes happened that Lloyd first printed his new taxa as *nomina nuda* in lists of determinations in replies to correspondents, published in his Mycological Writings as "Letters". Arising from this and the delay in publishing the descriptions of these new taxa it occasionally resulted in Van der Byl publishing the validating description prior to Lloyd's own account, e.g. as in *Daedalea fuscospora* Lloyd *apud* Van der Byl, *Polyporus glaucoporus* Lloyd *apud* Van der Byl, *Hydnum longospinosum* Lloyd *apud* Van der Byl, and *Guepinia agariciformis* Lloyd *apud* Van der Byl. In such instances Van der Byl presumably based his descriptions on the material available to him in his own herbarium and hence it seems reasonable to regard these collections as holotypes.

In this paper the genera are treated alphabetically as are the species within each genus except that the single species of *Polystictus*, i.e. *P. glaucoeffusus* Lloyd, is placed in the sequence of species of *Polyporus* and hence immediately precedes *Polyporus glaucoporus* Lloyd *apud* Van der Byl to which it is closely related. For every species the original diagnosis is reproduced, followed by my own observations. However, in those instances where both Lloyd and Van der Byl published accounts of the same taxa these have been combined such that the original data are followed by those of the subsequent author in round brackets. This was thought desirable as Lloyd's diagnoses were inclined to be brief and in need of supplementation.

Submitted for publication November 1971.

During the present study difficulty was sometimes experienced with the numbering of Van der Byl's specimens. For example in the case of *Polyporus rusticus* described by Lloyd in Mycol. Notes 53, p. 751, 1918, Van der Byl (1922) observed "Single collection from pine stump at Klampmuts, C.P.—(Cotype in Natal Herbarium, P.v.d.B. No. 387)" yet the specimen in his herbarium bears exactly the same collection data but is numbered 285. It frequently happened that while the collection data agreed with that published in Van der Byl's original diagnosis the numbers of the specimens in STE were different, e.g. the number of the type collection of *P. flexilis* Van der Byl was published as 810 yet the specimen in STE bears the number 894 and both were collected at Pietermaritzburg. Again with *Polyporus ochroporus*, Van der Byl emphasises that there was only a single collection from "a stump in Eastern Cape Forest Conservancy. Type in Natal Herbarium No. 115" yet the specimen in STE from Eastern Cape bears the number 130. These discrepancies appear to be due to a partial renumbering by Van der Byl of his herbarium when it was moved from Durban to Stellenbosch. Usually there is a specimen bearing the published number in PRU and a supplementary note on these collections will appear in due course.

ACKNOWLEDGEMENTS

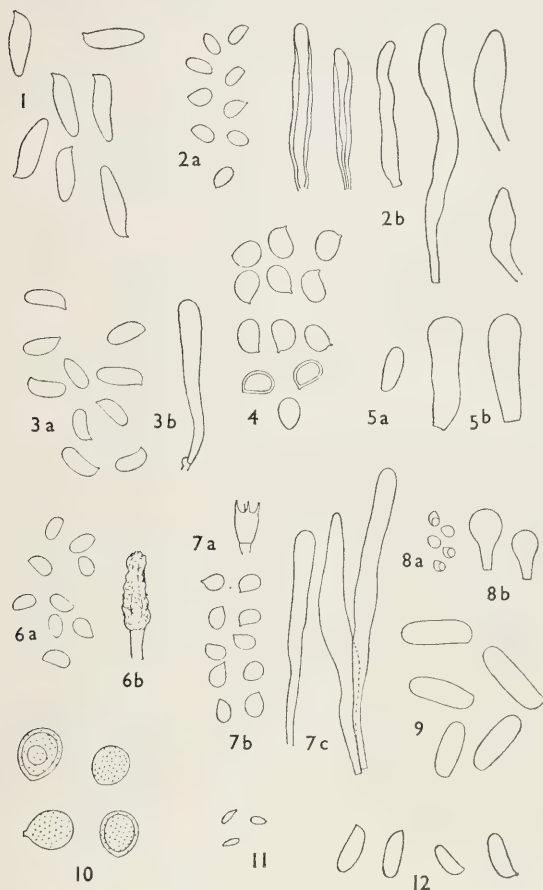
The author has great pleasure in thanking the trustees for the award of the Smuts Memorial Fellowship which made this work possible. He also wishes to thank Prof. E. A. Schelpe, University of Cape Town, who was responsible for suggesting and helping to organize my visit to South Africa to study the Basidiomycete Flora. Grateful thanks are also due to Prof. P. G. Jordaan, Head of the Dept. of Botany, University of Stellenbosch, for allowing me to work in his department and study the specimens in the Van der Byl Herbarium in his care, and also for his permission to publish this paper in English. It is also a pleasure to acknowledge the help and many kindnesses shown to me by Dr. J. G. Smith and the other members of the staff of the Botany Department of the University of Stellenbosch, as well as the associated members of the Department of Agriculture and in particular by Mr. Hugh Taylor.

AGARICALES

BOLETACEAE

Boletus stellenbossiensis Van der Byl in S. Afr. J. Sci. **22**, 167, 1925. (Fig. 1.)

"Plants stipitate; pileus firm, convex to expanded, 12 cm to 18 cm diam., 2 cm to 2,5 cm thick, upper surface glabrous, yellow to yellowish-brown, cracking into characteristic irregular areas; context cream to yellowish-brown in herbarium specimens, 2 mm to 1,5 cm thick, soft to hard; tubes up to 2 cm



FIGS. 1-12.

Fig. 1 *Boletus stellenbossiensis*—spores. Fig. 2 *Lentinus natalensis* (a) spores (b) cystidioles. Fig. 3 *Lentinus phillipsii* (a) spores (b) basidium. Fig. 4 *Daedalea fuscospora*—spores. Fig. 5 *Daedalea ligneo-texta* (a) spore (b) immature basidia. Fig. 6 *Daedalea rhodesiaca* (a) spores (b) encrusted cystidium. Fig. 7 *Fistulina africana* (a) basidium (b) spores (c) elements from pore mouth. Fig. 8 *Polyporus acaciae* (a) spores (b) capitate cystidioles. Fig. 9 *Polyporus argenteofulvus*—spores. Fig. 10 *Polyporus confragosus*—spores. Fig. 11 *Polyporus durbanensis*—spores. Fig. 12 *Polyporus glaucoporus*—spores. (All $\times 866$.)

long, approximately 2 to the mm, dark brown; stem central, rarely excentric, 2 cm diam., even or thickening upwards, solid, surface at times cracking lengthwise; spores yellowish, guttulate, 20 by 6 to 9, oblong-elliptic, with rounded ends.

Collected by the author on the ground in pine plantations at Klamputs (508), at Stellenbosch (815), between Stellenbosch and Somerset West (2 078).

The cracking of the upper surface of the pileus is characteristic and resembles the cracking of the upper surface of the pileus of the European *Annellaria separata*. The context is harder in specimens in which it is somewhat scanty and such specimens usually dry very hard."

Collection 815 was examined but unfortunately the specimens are in very poor condition and little can be added to the original data. The sporophores have pilei which are deeply areolately-cracked—the cracks being up to 2 mm deep. The areolae are smallest at the centre where they are about 3 mm wide and largest toward the margin where they are 6—8 mm wide. The cap appears to be more or less smooth and there is no obvious tomentum. The hyphae of the fruitbody are hyaline and lack clamp-connexions but there are some oleaginous hyphae with brown contents in the walls of the tubes. No cystidia were observed. The spores, which are pale yellowish-brown and of the usual boletoid shape, measured 13,0—15,6 (—18,2) $\times$ 4,0—5,0 μ .

It should be noted that Pearson (1950) also studied the material in STE and observed "that the spores are the typical boletoid subfusoid spores with one rounded end and the other with an oblique apiculus, and measuring 14—17 $\times$ 4—5 μ with a few larger. Probably it is the same as *B. curtipes* and both may only be sun-dried *B. edulis*." This suggestion that *B. stellenbossiensis* may be only sun-dried *B. edulis* is difficult to accept since there is no mention of any reticulum on the stem and one would hardly describe *B. edulis* as having a yellowish to yellowish-brown cap. Furthermore, the stem of *B. edulis* would normally be well in excess of 2 cm diam.

TRICHOLOMATACEAE

Lentinus natalensis Van der Byl in *Annale Univ. Stellenbosch* **2**, 4—5, 1924. (Fig. 2a—b).

"Fruitbody stipitate and growing on wood. Cap thin, leathery, pliable when wet, brittle when dry, infundibuliform, 5—6 cm diam., surface red-brown (terra cotta), covered with scattered bundles of rough, dark coloured hairs, striate from the centre to the margin and later splitting; margin thin, recurved, and covered with similar hairs. Gills decurrent down the stalk, pale, crowded, 1 mm or less in width, with entire margin. Stipe 1,5 cm long, 3—4 mm wide, hairy, more or less velvety, red-brown.

On dead stump, Winkelspruit, Natal (648).

This species differs from *L. velutinus* especially in the striate cap which later splits. Furthermore the colour is different and it is not as densely hairy. In dried specimens the surface of the cap is slightly grooved" [from the Afrikaans].

The type material consists of a single deeply infundibuliform fruitbody, 4.5 cm diam., which is sparsely covered with fascicles of hairs but was probably more conspicuously tomentose-hairy when young. It is now red-brown and neither sulcate nor striate even at the margin. The stipe is central, 2 cm long, 5 mm wide, and densely covered with red-brown hirsute-tomentum. The gills are decurrent, crowded, pale buff and without hyphal pegs. There are cystidioles in the hymenium, 22–64 μ in length, 6–8 μ in width, with refractive glassy contents. These vary in shape from small lanceolate organs to more elongate bodies with rather undulating outline resembling gloecystidia, others are somewhat narrower, 4.2 μ wide, subcylindric or slightly fusiform with thickened walls except toward the apex. The spores are small, hyaline, elliptic, 5.2–6.2 $\times$ 3.0–3.2 (—3.75) μ .

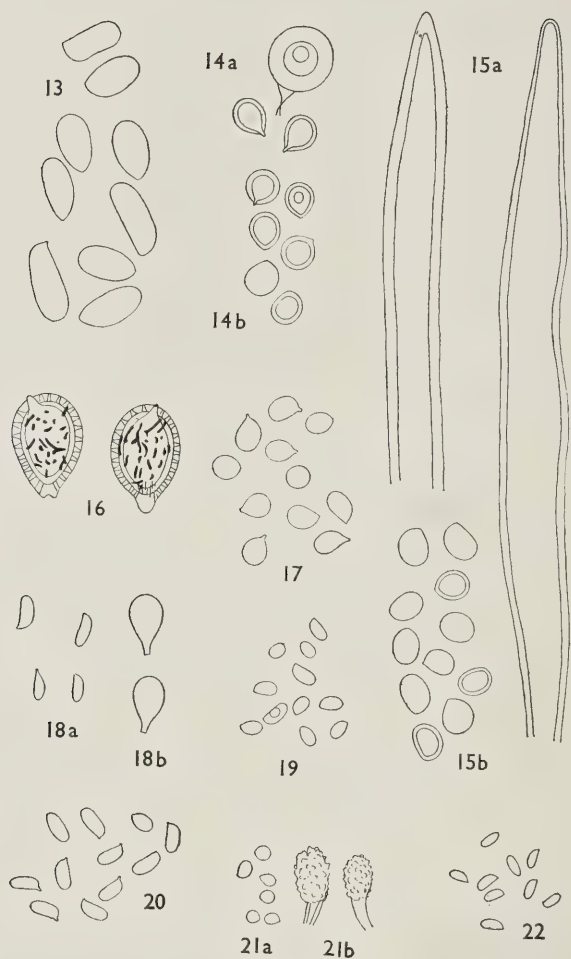
L. natalensis is best regarded as a synonym of the rather variable *L. velutinus* Fr. The differential characters emphasized by Van der Byl for his species are too unreliable to serve as the basis for the recognition of a distinct taxon.

Lentinus phillipsii Van der Byl in S. Afr. J. Sci. **23**, 284, 1926. (Figs. 3a–b; 35.)

"Pileus stipitate, orbicular, glabrous, leathery, chocolate brown, 2.5–6 cm. diam., margin incurved in drying, at times splitting from the margin inward. Flesh white. Gills slightly decurrent and forming areolae on the stem, 1 mm or less apart, 3 mm wide, yellowish salmon in dried material, edge entire. Stem excentric, solid, 1 cm long, narrowing to the base. Spores hyaline, oblong with rounded ends, 10 by 4 μ .

On old wood, Knysna. Leg. J. F. V. Phillips (2240)."

The type material, collected by Phillips, 18.9.1925, consists of sporophores with pilei 2.3–5.8 cm diam. These are not quite circular, since the fruitbodies evidently grew close to the substrate resulting in the caps becoming flattened behind. The pilei, which have an incurved margin, are grey-brown with the surface disrupted into rather inconspicuous adpressed scales exposing the pale flesh. In addition the surface of the cap is covered with dark cobwebby fibrils which form more or less dense fibrillose scales at the centre. The ochraceous-cream gills, which are not crowded, anastomose on the stem down which they are shortly decurrent. The stipe, about 1 cm long, is strongly excentric. Anatomically the fungus is formed of thick or thin-walled clamp-bearing generative hyphae, up to 8 μ wide, which eventually give rise to elongated thick-walled elements of similar width, tapering to a thin-walled apex. These terminal elements could be regarded as skeletal hyphae but the differentiation is but slight. The structure is perhaps best regarded as rudimentarily dimitic. The thick-walled



FIGS. 13-22.

Fig. 13 *Polyporus glauco-effusus*—spores. Fig. 14 *Polyporus nigro-applanatus* (a) ? chlamydo-spore (b) spores. Fig. 15 *Polyporus ochroporus* (a) setoid hyphae from dissepiments (b) spores. Fig. 16 *Polyporus reticulatosporus*—spores. Fig. 17 *Polyporus salisburyensis*—spores. Fig. 18 *Polyporus schreuderi* (a) spores (b) immature basidia. Fig. 19 *Trametes albotexta*—spores. Fig. 20 *Trametes griseo-lilacina*—spores. Fig. 21 *Trametes subflava* (a) spores (b) encrusted cystidia. Fig. 22 *Trametes varians*—spores. (All $\times 866$.)

elements have a glassy appearance in KOH and may possibly have been somewhat gelatinized by it. The hyphae forming the dark fibrils at the centre of the cap are thin-walled, $5-8\ \mu$ wide, and encrusted with brown pigment deposited in transverse bands. No cystidia were observed. The basidia are clavate with a basal clamp-connexion and measure $40 \times 5\ \mu$. The spores are thin-walled, hyaline, elliptical, $7.2-9.75 \times 3.5-4.2\ \mu$.

APHYLLOPHORALES

POLYPORACEAE

Daedalea fuscospora Lloyd *apud* Van der Byl in S. Afr. J. Sci. **21**, 308, 1924.

[First published by Lloyd in Mycological Writings 7, 1122, 1922 as a *nomen nudum*]. (Fig. 4.)

"Pileus annual, sessile, applanate, dimidiate, coriaceous-corky, drying firm, $9\text{ cm} \times 7\text{ cm} \times 0.4-1.5\text{ cm}$; surface rugulose, nigger brown, velvety to subglabrous; context brown, drying hard and brittle; tubes $0.5-0.9\text{ mm}$ long; mouths angular, poroid, becoming daedaleoid, greyish brown, averaging 1 to the mm; spores brown, guttulate, $5\ \mu-6\ \mu \times 8\ \mu$.

On old wood, Victoria Falls, Rhodesia (490)."

The name *D. fuscospora* was first introduced by Lloyd as a *nomen nudum*, in a list of determinations of fungi which were sent to him for naming by Van der Byl. However, when the latter published his validating description of the species he no doubt based this account on the specimens in his herbarium and hence the collection in STE should be regarded as the holotype and that in the Lloyd herbarium as isotype of the species.

According to Stevenson & Cash (1936), although Lloyd failed to publish a description of *D. fuscospora* he left fairly detailed notes with the material in his herbarium as follows:—"This is an exceptional plant difficult to place as to genus. As we recall the large pored species, with colored spores, only *Daedalea sprucei* of South America occurs to us. This African plant is not a good *Daedalea*, rather the type of a *Hexagona*, or large pored *Trametes*. The sinuate pores, however, place it in *Daedalea*, or rather *Phaeodaedalea* as McGinty calls the colored spored *Daedaleas*. Sessile, flat, about 1 cm thick. Surface with a dark, thin but distinct crust, glabrous but uneven. Context and pore tissue about Brussels brown. Pores large, irregular, sinuate, but probably better classed as an irregular *Hexagona* than as *Daedalea*. Setae none. Spores globose, $6-7\ \mu$, colored, smooth. We would place this in section 150 of *Daedalea*, though as previously stated, it is not satisfactory to class it in any established section."

The type material in STE, which has been treated with mercuric chloride, comprises a quite large sporophore, 8 cm wide, 6 cm from the point of attachment to the margin, with a dark, rusty-brown pruinose-tomentose covering over

an almost black horny, but thin cuticle, which shows in sections through the fruitbody as a pencil-thin line. The surface of the bracket is uneven and knobbly as well as concentrically sulcate. The flesh is dark ochraceous-brown; the tubes, up to 1 cm deep, have thin dissepiments; the pores are daedaleoid, on average about 1 mm wide, and brown with an ashy pruina. Anatomically the flesh is monomitic, consisting of brown generative hyphae, up to $7,5\ \mu$ wide, with thin or only slightly thickened walls; they are branched and septate but devoid of clamp-connexions. Spores are abundant, $7-9 \times 5-6\ \mu$, deep brown, with thickened walls, varying in shape from broadly elliptical to ovate.

The generic placement of this fungus presents considerable difficulty for although the genus *Phaeodaedalea* was validly published by K. Fidalgo (1961) as an entirely new genus, the type species was given as *Daedalea sprucei* Berk. This has a trimitic hyphal structure and although the spores were thought by Fidalgo to be 'globose or subglobose, not amyloid, yellowish brown, slightly apiculate, thickened, $9,5-11,5 (-13) \times 10,5-13,5 (-15)\ \mu$, with a smooth and brown outer layer, $1-1,5 (-2)\ \mu$ diam., not stained by phloxine, which however stains the interior of the spore dark pink,' these are not the basidiospores but conidia; the actual basidiospores being $4,0-4,5 \times 2,0-2,5\ \mu$, thin-walled, hyaline and elliptical. Clearly *D. fuscospora* cannot be accommodated in *Phaeodaedalea* Fidalgo since it differs so markedly from the type species in anatomy and spore characters. In some respects it suggests the genus *Inonotus* Karst.

Daedalea hobbsii Van der Byl in S. Afr. J. Sci. **18**, 287, 1922.

"Plants annual, sessile; pileus dimidiate, coriaceous to corky, imbricate, laterally connate, decurrent at attachment, 5 to 12 cm by 4 to 5 cm by 0,5 to 2 cm; surface white, finely tomentose to subglabrous, azonate, usually tuberculate, rarely smooth; context 0,4 to 1,4 cm fibrous, tough, soft when fresh, drying firm and corky, zoned, wood coloured, shining, shade varying with angle of light; tubes 2 to 5 mm long, elongated on decurrent portion, white within; mouths poroid and subrotund to elongated and daedaloid, 2 to 3 to the mm measured transversely; edges thick entire, white; spores hyaline, smooth, globose, 3 to 4 μ diam; hyphae simple 3 to 5 μ diam.

Distribution.—Found at Howick, Natal, by G. Hobbs. (Type in Natal Herbarium, No. 922.)

The context has a satiny lustre when smoothly cut and the shade of colour appears different according to the angle of the light."

The type material at STE is *Trametes meyenii* Kl. [Syn. *Trametes obstinata* Cooke]. This fungus was transferred to the genus *Cerrena* S. F. Gray by Hansen (1960), but the trimitic hyphal structure is not in accord with such a disposition as noted by Van der Westhuizen (1971). It is best left in the genus *Trametes* Fr., although it may ultimately have to be accommodated in *Coriolus* Quél. The spores noted by Van der Byl in the type material of *D. hobbsii* were almost certainly of



FIGS. 23–32.

Fig. 23 *Polyporus vicinus* (a) spores from Kew specimen No. 1153 (b) chlamydospores from specimen No. 1153 in Herb. STE (c) spores from specimen No. 1154 in Herb. STE. Fig. 24 *Fomes mesoleucus* (a) spores (b) chlamydospores [both from Type specimen in Herb. K.]. Fig. 25 *Vanderbylia unguolata* (a) spores $\times 1450$ (b) spores $\times 866$ [both from Type specimen in Herb. K.]. Fig. 26 *Vanderbylia fraxinea* (a) spores $\times 1450$ (b) spores $\times 866$ [both from Windsor Park, Berks. 4 Sept. 1958]. Fig. 27 *Vanderbylia latissima* (a) spores $\times 1450$ (b) spores $\times 866$ (c) thick-walled cystidia. [from African material in Herb. K.]. Fig. 28 *Polyporus rusticus*—spores. Fig. 29 *Odontia knysnana*—cystidiolate. Fig. 30 *Clavaria durbana*—spores. Fig. 31 *Guepinia agariciformis* (a) spores (b) immature basidium and septate paraphysis. Fig. 32 *Hydnum longispinosum* (a) immature basidia (b) spore (c) skeletal hypha from spine. (All $\times 866$ except where otherwise indicated.)

extraneous origin. The spores of *T. meyenii* measure 3,75—6,0 (—6,5) $\times$ 2,0—3,0 μ .

Daedalea ligneo-texta Van der Byl in S. Afr. J. Sci. **21**, 308, 1924. (Figs. 5, 36.)

"Pileus, sessile, woody, laterally elongated, broadly attached, narrow, 6 cm $\times$ 1 cm—2,5 cm $\times$ 1,5 cm; surface woody, glabrous, greyish, uneven and cracked; context hard, 5 mm—7 mm, light brown; tubes 3 mm—5 mm long, mouths irregular, dissepiments thick, rupturing and mouths then daedaloid.

Old wood, Knysna (1356), by A. E. van der Bijl.

Recognisable by woody, broadly attached pileus with greyish, uneven and cracked upper surface."

The type specimen, collected at Knysna, Jan. 1924, is a thick, creamy-white, woody fungus, with remarkably hard, lignicolourous flesh. The fruitbody consists of an effused resupinate portion, extending down over the substrate and bearing open 'pores', represented by thick, elongated, plate-like dissepiments. At its upper limit the fungus has grown out to produce a thick (—1,5 cm), narrow, convex pileus with downward curving margin. On the underside of the pileus the pores are represented at the margin by a series of radial plates which are often forked but these fuse behind to form small pores which are approximately 2 per mm. Hyphal structure is difficult to interpret owing to the extremely hard flesh, but this comprises thin-walled, clamp-bearing generative hyphae, and solid skeletal hyphae, 4—5 μ diam.; it is not certain whether binding hyphae are present. There is a well-developed hymenium formed of clavate basidia, 26,0 $\times$ 8,75 μ and these give rise to hyaline, elliptical spores measuring 10,5—12,0 $\times$ 4,0 μ . However, very few spores were seen and observation was hampered by the specimen having been poisoned with mercuric chloride.

Daedalea rhodesiaca Van der Byl in S. Afr. J. Sci. **22**, 167, 1925. (Fig. 6a-b.)

"Plants small, coriaceous, annual, sessile, effuso-reflexed, drying brittle; pileus imbricate, laterally elongated, 0,5 by 1 to 2 by 0,5 cm; surface strigose, yellowish-brown, fading to pale, faintly concentrically zoned; context brown, corky; tubes 2 mm to 3 mm long, approximately 1 mm across, dissepiments yellowish-brown, splitting and becoming irpicoid; spores not found.

Collected on old wood at the Victoria Falls, Rhodesia by the author (790)."

Most of the fruitbodies have a poroid hymenophore but in some the configuration is irpicoid. The hyphal construction of the yellowish flesh is virtually dimitic. The generative hyphae, 5 μ wide, have thickened yellowish-brown walls, but retain a wide lumen. These hyphae, which are septate, lack clamp-connections and are often branched. However, the terminal elements may be extremely long and unbranched and are indistinguishable from skeletal hyphae. Some of these skeletal hyphae enter the hymenium where they become modified to form small, lanceolate, encrusted cystidia. In addition similar cystidia originate from

generative hyphae just beneath the hymenium. Spores are numerous, hyaline, elliptical, and measure $5.0-7.0 \times 3.0-3.5 \mu$.

This is '*Irpex flavus* Kl.

Fistulina africana Van der Byl in S. Afr. J. Sci. **25**, 187, 1928. (Fig. 7a c.)

"Pileus stipitate, fleshy, subgelatinous in upper layer, subreniform to dimidiate, 3×5 cm, up to 2.5 cm thick; upper surface maroon coloured, rough with darker coloured, raised pustules; flesh colourless to ashy grey, not mottled with reddish spots, drying brownish; stipe short, lateral, up to 1 cm diam., with putty-coloured spots in the tissues; tubes up to 1 mm long, separate; mouths round, chocolate-coloured; spores $5-7 \times 3-4 \mu$, globose to ovoid or ellipsoid, yellowish-brown in mass, contents light yellowish, with a large central gutta. On trunks of living *Platylophus trifolius* at Knysna. Collected by J. F. V. Phillips in March, 1926 (2320), and by F. Laughton in April, 1928 (2504). This is the first record of a *Fistulina* from South Africa."

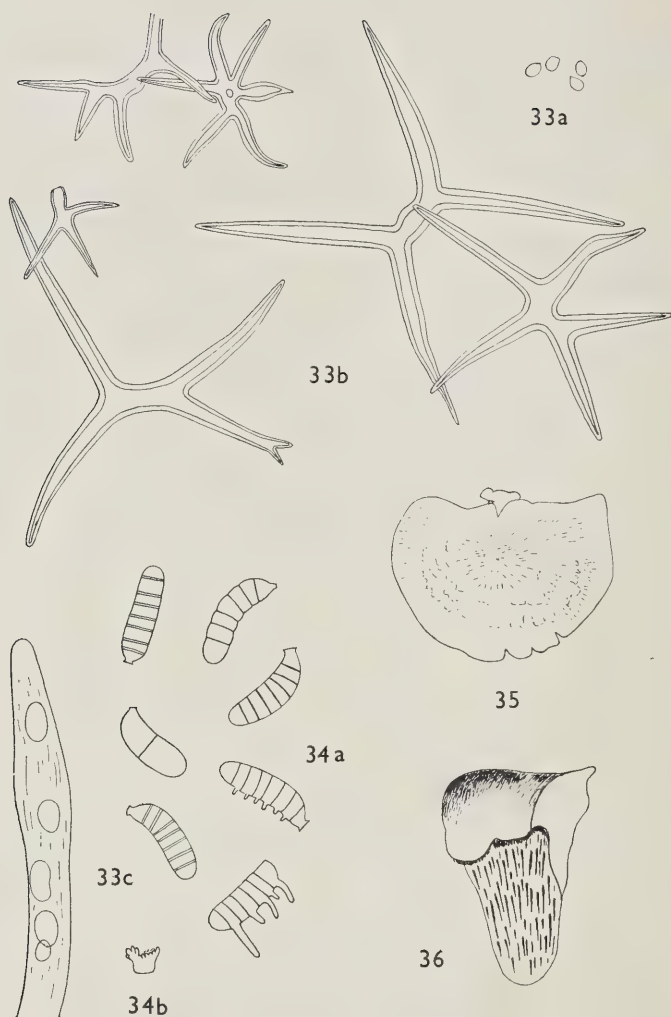
Collection No. 2320 is too shrivelled to give much idea of the appearance of the fresh plant. The hyphal construction is monomitic, consisting of very thin-walled, twisted, ribbon-like generative hyphae, some of which appear to bear clamp-connexions, although these are difficult to demonstrate. In addition there are broad conducting hyphae, 5μ wide, with coloured 'sap'. At the mouth of the tubes there are long clavate, cylindric or fusiform elements, $4.5-6.0 \mu$ wide, which taper toward the base and contain a coloured 'sap'. There is a thick horny layer at the surface of the pileus. In section this consists of a dense, dark-brown layer of horizontal hyphae. Above it the hyphae are somewhat disorientated but finally grow up vertically. In this latter zone some of the hyphae form dense tufts, which probably represent rudimentary pores as found on the surface of the European fungus *F. hepatica* Schaeff. ex Fr. The basidia, $6.2 \times 5.75 \mu$, are short and squat with 4 sterigmata. The spores, $5.0-6.0 \times 4.0-4.5 \mu$, vary from ovate to broadly elliptical or elliptical.

F. africana is certainly correctly assigned to the genus *Fistulina* Bull. ex Fr. It appears to differ from *F. hepatica* in the lack of red flesh and in having chocolate-coloured pores.

It should be noted that in addition to the collections cited by Van der Byl there are 2 further gatherings in STE from Knysna collected by F. S. Laughton in April, 1924 and January, 1929.

Irpex africanus Van der Byl in Annale Univ. Stellenbosch **12**, 5, 1934.

"Fruitbody sessile, pileate. Pileus coriaceous, firmer when dry, imbricate, 1.5-3 cm from the substrate, 3 cm broad, narrowing behind to 1.5-3 cm; upper surface glabrous, cinnamon to sandy-brown; shining with concentric zones, smooth or rough. Context 0.75-2 mm thick, cinnamon-coloured. Hymenophore tubular; tubes 0.25-0.75 mm long; pores irregular, angular, 3-4 to the mm, cinnamon to sandy-brown, later becoming toothed.



FIGS. 33-36.

Fig. 33 *Lachnocladium cristatum* (a) spores (b) stellate elements forming context of main branches (c) gloeocystidium. Fig. 34 *Dacrymyces australis* (a) spores, two of which have germinated (b) habit sketch of fruitbody $\times 1$. Fig. 35 *Lentinus phillipsii*—habit sketch $\times 1$. Fig. 36 *Daedalea ligneotexta*—habit sketch $\times 1$. (All $\times 866$ except where otherwise indicated.).

On rotten wood. No indication where it was collected." (From the Afrikaans).

The specimens so named in STE bear the No. 539 and consist of poorly preserved flabellate sporophores, which are reduced behind to a narrow point of attachment. The brackets, which are more or less imbricate, have a mid-brown surface with a dark blackish-brown margin. They are zoned and have a silky sheen but are ornamented with adpressed spiculate processes which are a marked feature of some fruitbodies though less well developed in others. The pores, often absent from the marginal zone, are small and become toothed and irpicoid with age. Anatomically the flesh is trimitic, comprising skeletal hyphae, up to 8 μ diam., many of which are thin-walled or have a broad lumen, and coralloid binding hyphae which are virtually solid; generative hyphae were not actually demonstrated. There was no hymenium present and no cystidia or spores were seen.

This fungus belongs in the genus *Coriolus* Quél. and is reminiscent of *C. friesii* (Kl.) Pat.

Polyporus acaciae Van der Byl in S. Afr. J. Sci. **22**, 168, 1925. (Fig. 8a-b.)

"Plants annual, sessile; pileus ochraceous, coriaceous, drying firm and brittle, at times imbricate and laterally connate, dimidiate or prolonged radially; surface azonate, finely velvety tomentose, 0,5 cm to 1,5 cm by 0,5 cm to 1 cm by 0,2 cm; context 1 mm thick, corky, light yellow; tubes 1 mm long; pore mouths irregular, subrotund to angular, 4 to 6 to the mm; spores not found.

Common on stumps of *Acacia mollissima* at Krantzklouf, Natal, where it was collected by the author (773).

This plant agrees in general with *Polyporus subiculoides* recently named from South Africa by Mr. C. G. Lloyd, but differs from it in that it has no subiculum."

The above material consists of narrow, entirely buff-coloured brackets with a minutely felty-tomentose surface, and an hymenophore comprising minute pores, 5-6 per mm. The brackets measure 1,2 cm from the point of attachment to the margin. The context consists of hyaline hyphae, 2,5-3,0 μ wide, with thickened walls although retaining a wide lumen, and bearing small clamp-connexions at the septa. In the dissepiments there are also rather long, unbranched similar hyphae and the structure here could be interpreted as dimitic. There are capitate cystidioles in the hymenium about 15 μ long with heads about 8 μ diam. The spores are hyaline, and vary from ovate to broadly elliptical, and measure 3,2-3,75 $\times$ 2,2-2,5 μ .

This is *Polyporus subiculoides* Lloyd as Van der Byl has, himself, noted on the packet. The fungus belongs in the genus *Xylodon* Karst. together with *X. versipora* (Pers.) Bond.; the transfer having been made by Reid (1969). For full

cultural data see Van der Westhuizen (1971). See also under *Polyporus trichiliae* Van der Byl.

Polyporus argenteofulvus Van der Byl in S. Afr. J. Sci. **24**, 225, 1927. (Fig. 9.) *Amauroderma argenteofulvum* (Van der Byl) Doidge in Bothalia **5**: 503, 1950.

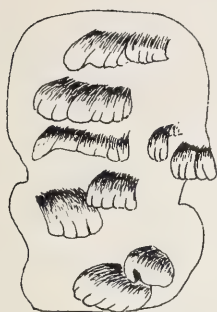
"Pileus annual, stipitate, umbrella-shaped, depressed in the centre, glabrous, even, 5 cm diam., silvery-brown, with darker hazel-brown concentric rings; context white, corky, up to 2 mm thick, with two brown coloured rings running from the stalk to near the periphery of the pileus; tubes yellowish-brown, 5 to 9 mm long; mouths angular, 2 to 3 to the mm, dissepiments thin; spores light yellow, oblong with rounded ends, 16 to $18\ \mu$ by $6\ \mu$; stipe central 3 cm long, 5 mm diam., silvery brown. At Salisbury, Rhodesia. F. Eyles 4110. (2421)."

The cap, 4.5 cm diam., is convex, umbilicate and ochraceous with numerous distinct darker zones which are closest together at the margin. Within the umbilicus there are a few innate spiculose fibrils. There is a short stipe 3 cm long, 1 cm wide, which narrows above. The context of the cap is pale and marked with two dark, horny lines in the middle extending from the centre of the pileus almost to the margin. The hyphal structure is dimitic, consisting of thin-walled, branched, clamp-bearing generative hyphae, and very long, solid, unbranched skeletal hyphae, $5\ \mu$ wide. The spores, 14.0 — 18.2×4.5 — $6.0\ \mu$, are thin-walled, hyaline to distinctly brownish, and either subcylindric or narrowly elliptical.

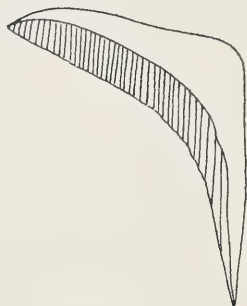
Polyporus confragosus Van der Byl in S. Afr. J. Sci. **24**, 225, 1927. (Fig. 10.)

"Pileus annual, stipitate, orbicular to umbrella-shaped, fawny-brown, velvety to subglabrous, irregularly furrowed radially; uneven, 2 to 10 cm diam., 5 to 7 mm thick individual pilei at times coalesce; context amber yellow, corky, 2 mm thick; tubes hazel-brown, 3 to 4 mm long; mouths putty coloured, 4 to 5 to the mm, irregular; spores lightly coloured, subglobose, smooth, $12\ \mu$ diam.; stipe central, 2 to 3 cm long, 0.5 to 1 cm diam., dark brown. Rhodesia. F. Eyles 4111 (2422)."

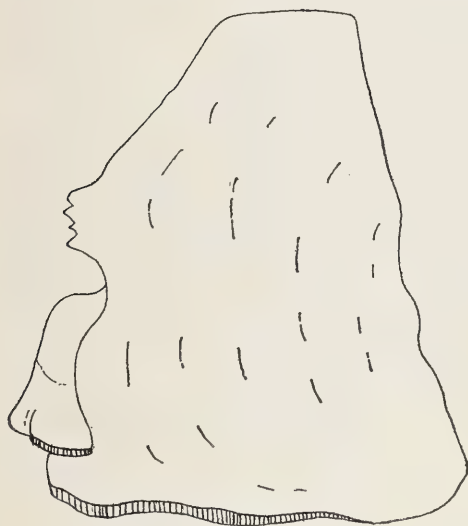
The above material consists of stipitate sporophores with caps 2.5—8.0 cm diam. In one instance the sporophore is a compound structure involving 4 fruit-bodies and it is possible to make out 4 fused or semi-fused stalks up to 3.5 cm long. The ochraceous-buff caps are convex, slightly depressed at the centre, concentrically sulcate and radially wrinkled or knobbly. There is a well-marked raised ridge around the depressed centre, and the surface of the pileus is ornamented with alternating matt and greasy-shining zones. The context is brownish with a dark line along the central portion. It consists of clamp-bearing generative hyphae and thick-walled hyphae, $6\ \mu$ diam., with a wide lumen, which are repeatedly branched and finally terminate in elongated whip-like endings. These hyphae are best regarded as Bovista-type binding hyphae rather than arboriform skeletals. Spores are present which vary in shape from globose to ovate.



37



38



39



40

FIGS. 37-40.

Fig. 37 *Polyporus durbanensis*—habit sketch. Fig. 38 *Trametes salebrosa*—section through fruitbody. Fig. 39 *Trametes subflava*—section through fruitbody. Fig. 40 *Polyporus schreuderi*—habit sketch. (All $\times 1$).

They have a distinct wall which is minutely punctate, and are pale straw-coloured; they measure $10,5-12,0 \times 9,0-10,5 \mu$.

This fungus clearly belongs in the genus *Amauroderma* (Pat.) Torrend and is accordingly so transferred as *Amauroderma confragosus* (Van der Byl) Reid, comb. nov.

Polyporus durbanensis Van der Byl in S. Afr. J. Sci. **18**, 261-262, 1922. (Figs. 11, 37.)

"Plants annual, sessile or effused reflexed; pileus dimidiate, imbricate, applanate to conchate, laterally connate, 1 cm to 3 cm by 0,5 cm to 2,5 cm by 0,1 cm to 0,3 cm, coriaceous, tough, becoming firm and rigid in drying; surface pearl to lead or ash grey, finely tomentose pruinose, undulating, smooth becoming scabrid and fuliginous in places; context 0,5 mm to 1,5 mm white to discoloured, firm, corky; tubes 0,5 mm to 1,5 mm long; mouths irregular, angular, 4 to 5 to the mm; edges thin, entire, grey changing to yellowish; spores hyaline, globose to oblong, 4μ diam., hyphae 4μ to $5,5 \mu$.

Distribution.—Known only from around Durban where it was collected on dead logs by the writer. (Type in Natal Herb. P. v.d. B., No. 896.)"

The collection in STE, No. 571, is clearly not the type but nevertheless it was collected by Van der Byl at Durban and agrees with the original diagnosis in most respects. The fruitbodies consist of a subiculum growing over the vertical surface of the host and arising from it are numerous small, discrete brackets, up to 1,8 cm wide and about 1 cm from the point of attachment to the margin. The pilei, more or less convex, with a downwardly curved and inconspicuously radially plicate margin, have a smooth pruinose-scurfy-tomentose, grey-buff surface. The concolorous pores are very small and just about visible to the naked eye. The hyphal structure of the context is trimitic comprising thin-walled, hyaline, clamp-bearing generative hyphae, coralloid binding hyphae, $2,5-3,0 \mu$ wide, and unbranched, virtually solid skeletal hyphae, $5-6 \mu$ wide. No cystidia were seen. Scanty spores were present but these were mostly collapsed. They were small, elliptical, $4,0-4,75 \times 1,0-2,0 \mu$, and seemed to belong to the fungus in question.

Clearly this collection represents a fungus belonging to the genus *Coriolus* Quél., but before any transfer is made it will be necessary to confirm any such disposition by a study of the type material.

Polyporus flexilis Van der Byl in S. Afr. J. Sci. **18**, 271, 1922.

"Plants effused-reflexed; pileus coriaceous, imbricate, tough, at times conchate, laterally extended, connate, 1 cm to 7 cm by 1 cm to 1,5 cm by 0,1 cm to 0,5 cm; surface with a brown velvety to hirsute pubescence, azonate; margin thin, acute, often turned upwards; context soft and spongy to corky, 1 mm to 4 mm, umber brown, shining, fibrous; tubes 0,3 mm to 1 mm long, concolorous with context, elongated on effused portion; mouths subrotund to elongated or

angular, 2 to 3 to the mm; edges entire, thin, brown; hyphae simple $4\ \mu$ to $5\ \mu$.

Distribution.—Found at Pietermaritzburg, Natal, on log, by the writer.

The plant is related to *Polystictus zelanicus*, and differs from *Trametes protea*, Berk., in colour of context. (Type in Natal Herbarium, P. v. d. B., No. 810.)"

A specimen in STE, No. 894, determined by Van der Byl and collected by him at Pietermaritzburg, consists of fruitbodies forming long, narrow, effuso-reflexed brackets, prolonged behind into a resupinate portion. The brackets are 4—5 cm long, but only 1.0—1.5 cm from the point of attachment to the margin. At the surface the pileus is covered with a warm brown tomentum, which appears shaggy under a lens. The pores are similarly coloured and are 2—3 per mm, but there is a non-poroid, sterile marginal zone. The flesh is cottony and warm olive brown. Anatomically the context is clearly trimitic, comprising branched, thin-walled generative hyphae, 3—4 μ wide, with clamp-connexions, dense clumps of coralloid binding hyphae, 2.5—3.0 μ wide, and long, unbranched skeletal hyphae, 5—6 μ wide, with rather thick brown walls but retaining a wide lumen. No cystidia or spores were seen.

This is probably the same as *Funalia protea* var. *imbricata* (Berk.) Reid, comb. nov. [Basionym: *Polyporus proteus* var. *imbricatus* Berk. in Hooker's Lond. J. Bot. 2, 516, 1843] but in the absence of spores one cannot be absolutely certain for the reasons outlined under *P. glauco-effusus* Lloyd; see also under *P. glaucoporus* Lloyd, *P. livingstoniensis* Van der Byl and *P. rusticus* Lloyd.

It should be noted that in addition to the above collection there is another gathering in STE. This material (No. 578) was also determined by Van der Byl.

Polystictus glauco-effusus Lloyd in Mycological Writings 7, 1334, 1925 (Fig. 3074).

Polyporus glauco-effusus (Lloyd) Van der Byl in S. Afr. J. Sci. 23, 289, 1926. (Fig. 13.)

"Pileus effuso-reflexed, elongated, about an inch wide. Surface finely pubescent, light ochraceous brown, not zoned. Context thin, isabelline. Pores glaucous grey, minute round, or elongated (according to position). No cystidia or spores seen, but the white hymenium has numerous projecting hyaline hyphae. When we saw this specimen the glaucous grey pores recalled to us at once *Polystictus glaucoporus*, which we named recently for Prof. Bijl (compare page 1334), but on comparison we find an entirely different habit and pileus surface. This we would enter in Section 111 (rather than in 117)".

This fungus is extremely similar to *P. flexilis* Van der Byl in appearance and structure and also to *P. glaucoporus* Lloyd, *P. livingstoniensis* Van der Byl and *P. rusticus* Lloyd. It should be noted that Lloyd's observation that *P. glauco-effusus* has an entirely different habit and pileus surface from that of *P. glau-*

coporus is not borne out by a study of the type collections of these two species in STE. However, it must be admitted that Lloyd's photograph of the type material of *P. glaucoporus* (fig. 3080) shows almost dimidiate fruitbodies whereas the material of the same collection in STE consists of elongated brackets. Nevertheless, although *P. glauco-effusus* and *P. glaucoporus* appear so similar to the eye, they differ in spore characters, for although both have hyaline elliptical spores, in *P. glauco-effusus* they measure $15,5-17,75 \times 5,0-6,5$ (-8) μ , in *P. glaucoporus* they have a range of $8,75-11,5 \times 3,2-4,2$ μ . The fact that there is this spore difference makes it difficult to assign the other similar species to synonymy when the type material is sterile (as in *P. flexilis* and *P. livingstoniensis*). Notwithstanding, it would seem that the smaller spored fungus inclusive of *P. glaucoporus* and *P. rusticus*, is by far the most common and widespread in tropical and subtropical regions of the world and is best referred to as *Funalia protea* var. *imbricata* (Berk.) Reid. Since this fungus is so abundant in South Africa it would seem preferable to relegate the species based on sterile material to synonymy under the latter name, albeit with a point of interrogation. *P. glauco-effusus* also belongs in the genus *Funalia* Pat. but there is an older name for this fungus viz. *Polystictus argenteus* Lloyd which is hereby transferred to that genus as *Funalia argentea* (Lloyd) Reid, comb. nov. [*Polystictus argenteus* Lloyd in Mycological Writings 7, 112, 1922].

Stevenson & Cash (1936) have pointed out that owing to a typographical error, the specific epithet was originally published as *glauco-effuses*, as indicated by the correct legend to fig. 3074, and in the original manuscript of the published note. These authors also indicated that the type specimen [No. 53641 in the Lloyd Herbarium] is the collection bearing Van der Byl's No. 1470. Doidge (1950) added that this material was collected on poles of *Eucalyptus* sp. at Woodbush (Transvaal.) The type material in STE bears the following data "On *Eucalyptus* pole, Tzaneen Plantation, Transvaal, July 1924."

Polyporus glaucoporus Lloyd *apud* Van der Byl in S. Afr. J. Sci. **21**, 313, 1924. *Polystictus glaucoporus* (Lloyd *apud* Van der Byl) Lloyd in Mycological Writings 7, 1334, 1925 (Fig. 3080). (Fig. 12).

"Plants annual, sessile, thin; pileus coriaceous, applanate, imbricate, laterally connate, 3 cm—4 cm $\times$ 3 cm $\times$ 0,1 cm—0,3 cm; (Thin, applanate, rigid, sessile.) surface yellowish, tomentose, becoming rugulose-fibrillose in older regions; (Surface pale, dull, rugulose.) context brown, thin (Context brown.) tubes 1 mm—2 mm long, strongly glaucous within, mouths subrotund to angular or elongated radially (Pores small, elongated, angular, strongly glaucous.) dissepiments thin, splitting. (Cystidia none. Spores not found.).

Victoria Falls, Rhodesia (1066).

Recognisable by its strongly glaucous tubes."

Lloyd (1925) noted "What confusing situations do come up in classification!

Here we have a plant that we are convinced is a *Hexagona* as to relations, the section *Tenuis*, the same in everything excepting in its pores, and *Hexagona* is based on pores". He continued "We enter this in Section 117 with *Polystictus luteo-olivaceus*, but to our mind this section is more closely related to the section *Tenuis* of *Hexagona* than to *Polystictus*, excepting as to pores. The word *Polystictus* has a usual meaning of flexibility, which is just the contrary of this group of plants."

The type material in STE, consists of long brackets up to 7 cm in length and 3—5 cm from the point of attachment to the margin, with a pale buff to ochraceous-buff surface which is tomentose especially toward the margin but elsewhere rough with innate fibrillose strands or with a few spiculose processes at the extreme base. In one sporophore regeneration has occurred from an old dark blackish-brown basal portion. The flesh is olive-brown; the pores, 2—3 per mm, are very strikingly glaucous or ashy-grey; and the fruitbodies are flexible. Anatomically the hyphal structure is trimitic as in *P. flexilis* Van der Byl. There are very scanty and possibly immature spores present which are hyaline, elliptical and measure $8,75-11.5 \times 3,2-4,2 \mu$.

This is *Funalia protea* var. *imbricata* (Berk.) Reid. For further discussion of this and allied species see under *P. flexilis*, *P. glauco-effusus* Lloyd, *P. livingstoniensis* Van der Byl, and *P. rusticus* Lloyd.

Polyporus livingstoniensis Van der Byl in S. Afr. J. Sci. **22**, 168-169, 1925.

"Plants annual, sessile; pileus dimidiate, coriaceous, 1,5 cm to 3,5 cm by 0,7 cm to 2 cm by 0,3 cm; surface azonate, light grey, rugulose, hirsute; context brown, 1 mm thick, tubes 1 mm to 2 mm long, glaucous within, mouths irregular 1 to 2 to the mm; dissepiments thin, splitting; spores not found.

Collected on dead wood at the Victoria Falls, Rhodesia, by the author (799).

Polyporus glaucoporus, Lloyd and *Polyporus glauco-effusus*, Lloyd, have glaucous tubes with smaller pore mouths than *P. livingstoniensis*. The surface of the last-named is also more strongly hirsute and rougher to the touch."

The type material is very similar indeed to *P. flexilis* Van der Byl, *P. glauco-effusus* and *P. glaucoporus*. The pileus is attached by a dorsal boss and has a whitish, densely spiculose-roughened surface. The pores, which are strikingly ashy-grey, are larger than those in the three above-mentioned species, being 1 per mm. The flesh is olive-brown and trimitic as in these species. Spores were not seen.

This is probably *Funalia protea* var. *imbricata* (Berk.) Reid. See also under *P. flexilis*, *P. glauco-effusus*, *P. glaucoporus*, and *P. rusticus*.

Polyporus nigro-applanatus Van der Byl in S. Afr. J. Sci. **21**, 311, 1924. (Fig. 14 a-b.)

"Pileus sessile, applanate, woody, 31 cm $\times$ 19 cm $\times$ 0,8 cm—3,5 cm; surface horny encrusted, black, tuberculate; context creamy, fibrous-floccose, corky,

drying hard, 0.5 cm—1 cm thick; tubes 2 mm—7 mm long, creamy to brownish in herbarium specimens; mouths angular, irregular, light cinnamon, 2—5 to the mm; edges entire; spores lightly coloured, globose $10\text{ }\mu\text{—}14\text{ }\mu$ diam.

A single collection in bush at Durban, Natal (808).

Easily recognized by its black surface and relative large spores.”

The type material at STE has a smooth, black, horny surface, ligniculous flesh and similarly coloured but slightly more greyish-buff pores, which are invisible to the naked eye. It has a hard, woody texture and the tubes, up to 7 mm long, are not stratified. Hyphal structure of the flesh is difficult to interpret owing to its hard woody consistency. No generative or binding hyphae could be demonstrated but solid dextrinoid glassy skeletal hyphae, up to $8\text{ }\mu$ diam., appear to comprise the context. No cystidia were seen. Spores were abundant $8\text{—}9 \times 7\text{—}8\text{ }\mu$, varying in shape from globose to ovate, with thickened dextrinoid walls. In addition there are in the hymenium large thick-walled globose spores, measuring $14.2\text{ }\mu$ diam., which are probably chlamydospores. It was the latter which Van der Byl mistook for the spores of this fungus.

P. nigro-applanatus appears to be the same as that described a month previously by Lloyd as *P. vicinus* q.v. and which has been made the type species of the new genus *Vanderbylia* Reid.

Polyporus ochroporus Van der Byl in S. Afr. J. Sci. **18**, 269, 1922. (Fig. 15a-b.)

“Pileus sessile, convex above, thickest behind, 5.5 cm by 4 cm by 0.5 cm to 2.5 cm; surface brown, soft, minutely pubescent; context 0.5 cm to 2.3 cm, soft, tough, yellowish-brown above, dark-brown and brittle below, zonate, shining; tubes 1 mm to 7 mm long, ochre yellow, brittle, rigid brown hyphae in the walls; mouths angular averaging 2 to the mm, edges thin, entire to dentate, concolorous with tubes, changing to brown; spores lightly coloured, subglobose to elliptical, $4\text{ }\mu$ to $5\text{ }\mu$ by $5\text{ }\mu$ to $7.5\text{ }\mu$; setae scanty $15\text{ }\mu$ to $21\text{ }\mu$ long by $4\text{ }\mu$ to $7\text{ }\mu$ diam.; hyphae $4\text{ }\mu$ to $8\text{ }\mu$.”

Distribution.—A single collection from a stump in Eastern Cape Forest Conservancy was made by the writer. (Type in Natal Herbarium, P. v. d. B., No. 115).

The plant is evidently related to *P. patouillardii*, but with different surface, different colour of mouths, duplex context, larger pore mouths and thinner setae. The rigid hyphae in the walls of the tubes are less abundant than in the specimens of *P. patouillardii*.”

There is in STE a specimen of *P. ochroporus* determined by Van der Byl from the Eastern Cape but bearing the No. 130. This agrees in macroscopic features with the original diagnosis. It has large setoid hyphae $300\text{ }\mu$ long and up to $13\text{ }\mu$ wide, in the dissepiments. These elements, which may protrude into the tubes, taper to a narrow point of origin and have a pointed apex. Normally similar

setoid hyphae are found on the surface of the pileus in this species [Pegler (1964)] but no trace of any such hyphae were observed in this material. Setae could not be demonstrated in the tubes despite Van der Byl having observed them in the type material. Spores were abundant, $7-9 \times 6-7 \mu$, and broadly elliptical but sometimes almost subglobose, and with slightly thickened walls.

A second collection on *Salix* sp., Pietermaritzburg, coll. W. G. Rump (2768), Jan. 1935, is also preserved at STE. This too shows setoid hyphae in the tubes but none on the cap surface and again setae appear to be lacking in the hymenium.

This fungus belongs in the genus *Inonotus* Karst. and was so transferred by Pegler (1964).

Polyporus reticulatosporus Van der Byl in S. Afr. J. Sci. **24**, 225-226, 1927. (Fig. 16.)

"Pileus annual, stipitate, umbrella-shaped, 2 to 5 cm diam., 1 to 1.5 cm thick, yellow-ochre; context 2 to 6 mm thick, deep cream, corky; tubes 0.4 to 1 cm long, brownish-yellow (probably white in fresh specimens); mouths yellowish-white, irregular, 3 to 4 to the mm; spores papillate, reticulately marked, faintly coloured, sulphury-yellow in mass, 24 to 28μ by 16μ ; stipe central, 6 to 7 cm long, 0.5 to 1.5 cm diam., reddish-brown, varnished (lower part covered with sand). On dead wood at Salisbury, Rhodesia. F. Eyles 4121. (2419)."

The above material, collected in January 1925, consists of centrally stipitate fruitbodies with caps 2.0-5.5 cm diam., having a yellowish-ochre surface, which may be either matt or more or less shining. According to Eyles' notes the pileus of the fresh plant was "pale brown to cream, stipe with blood cold 'varnish' below cap, hymenium grey white. . . ." Anatomically the context consists of generative hyphae and skeletal hyphae up to 10.5μ wide, which are solid, glassy, subhyaline and seemingly occasionally branched. Also present are long, tapering, hyaline, scantily branched binding hyphae, about 2.5μ wide, of the Bovista-type. [It is just possible that these could be the arboriform endings of the skeletal hyphae or of certain skeletal hyphae]. The spores, $25.0-26.0 \times 15.6-16.0 \mu$, are pale straw-coloured, and of the typical *Ganoderma*-type, ornamented with a very broken reticulum of rods, lines, and isolated dots.

This fungus belongs in the genus *Ganoderma* Karst. and is hereby transferred to that genus as *Ganoderma reticulatosporus* (Van der Byl) Reid, comb. nov.

Polyporus rusticus Lloyd in Mycological Writings **5**, Mycological Notes No. 53, p. 751, 1918 (Fig. 1124). (Fig. 28).

"Sessile dimidiate. (Plants annual, sessile;) Surface rugulose, scrupose. (pileus corky, firm, rigid, circular to dimidiate 1.5 cm to 4 cm by 0.5 cm to 2 cm by 0.2 cm to 0.6 cm; surface grey, rugulose, scrupose;) Context hard, sublignous. Brussels brown. (context 3 mm to 4 mm fibrous, tough, corky, dark brown; margin acute, thick;) Pores rigid, small, with tissue paler than the context.

Mouths concolorous. (tubes 1 mm to 2 mm long, lighter than context; mouths irregular, angular to elongated, approximating 2 to 3 to the mm elongated as much as 2 mm; edges thick, firm;) Setae none. Spores cylindrical, $3,5 \times 8$, lateral, apiculate, hyaline (Spores (teste Lloyd) hyaline, cylindrical, obliquely apiculate, $3,5 \mu$ by 8μ ; setae absent; hyphae 4μ diam.)"

Van der Byl added "*Distribution*.—Single collection from Pine stump at Klappmuts, C.P. made by the writer. (Cotype in Natal Herbarium, P. v. d. B. No. 387).

The rough scrupose surface is peculiar. The pore mouths are frequently much elongated, and would suggest that the fungus may possibly occur in the lenzitoid form."

Lloyd also observed "I would enter this in Section 95, although the hard context and generally rigid nature suggest *Trametes*. I do not know any other species with same context color."

The specimen, in STE, although "on stump of *Pinus* sp., Klappmuts, C.P." bears the No. 285. This collection is surely only a slightly thicker non-flexible form of *Funalia protea* var. *imbricata* (Berk.) Reid in which the surface of the fruitbody is pallid and more or less spiculose behind, but brown and tomentose toward the margin. The pores, 2—3 per mm are brown, having lost their glaucous appearance due to weathering. Anatomically the context is trimitic as in *P. flexilis* Van der Byl, but binding hyphae are not very abundant.

There are hyaline elliptical spores measuring $7,5-9,0 \times 3,0-4,0 \mu$.

For a further discussion of related species see under *P. flexilis*, *P. glaucoeffusus* Lloyd, *P. glaucoporus*, and *P. livingstoniensis*.

Polyporus salisburyensis Van der Byl in S. Afr. J. Sci. **24**, 226, 1927. (Fig. 17.)

"Pileus annual, stipitate, orbicular, 5 to 9 cm diam., 0,7 to 2 cm thick, maize yellow, margin blackening when touched (in fresh specimens); context 0,5 to 1,8 cm thick, dark fawn, corky; tubes up to 2 mm long; mouths ashy-grey to darker where bruised, minute, irregular, 5 to 6 to the mm., dissepiments thick; spores scanty, ovate to elliptic, faintly coloured, 5×6 to 8μ diam., stipe central, 4 to 7 cm long, up to 1 cm diam., umber-brown. On the ground at Salisbury, Rhodesia. F. Eyles 4220. (2437)."

The collector's note on the type material in STE states: "Hard, rigid, 4—5 cm height above ground, up to 9 cm diam. Pileus centre light brown, dry, slightly concave, margin slightly raised, 10—15 mm wide, bright sulphur yellow, turning black where touched. Context blood red, turns black, up to 20 mm thick. Tubes at deepest 2 mm, minute. Hymenium dull creamy grey. Stipe 10 mm diam. at top, hard."

The specimens now are centrally stalked with a single stipe or with two stipes fused below and becoming slightly separated above, but the pileus then shows no sign of its dual origin. The pileus, 5—6 cm diam., and 1,5 cm in total thickness,

has an ochraceous-brown, scurfy-pruinose surface and a very obtuse margin. Pores are not visible to the naked eye but the hymenophore is brownish-grey with dark areas suggestive of bruising. The flesh is ochre-brown and there is only a poorly developed cuticle. The tubes are very shallow, up to 1 mm deep. The stipe is warm brown with a scurfy-pruinose surface. Anatomically the context of the pileus has a dimitic structure consisting of clamp-bearing generative hyphae and skeletal, $4-5\ \mu$ wide, with thick, subhyaline or pale brown walls, and with very much branched arboriform endings, which resemble *Bovista*-type binding hyphae. In the upper part of the tubes the skeletal have thick-walled, obtuse or more rarely fusiform endings. Where they grow down the length of the tube they are about $5\ \mu$ wide, unbranched and have rather thin brown walls and a very wide lumen. However, toward the mouth of the tubes the tissue is entirely composed of thin-walled actively growing hyphae. No cystidia were seen but spores are abundant, $6.2-8.0 \times 4.5-6.0\ \mu$, smooth, hyaline, varying in shape from broadly elliptical to ovate.

This fungus is best assigned, at least for the present, to the genus *Amauroderma* (Pat.) Torrend, as *Amauroderma salisburyensis* (Van der Byl) Reid, comb. nov.

Polyporus schreuderi Van der Byl in S. Afr. J. Sci. **21**, 311-312, 1924. (Figs. 18a-b; 40.)

"Pileus sessile, sometimes laterally connate, applanate or horseshoe shaped, at times attenuated at attachment, $0.9\text{ cm}-2\text{ cm} \times 2\text{ cm} \times 0.4\text{ cm}$; surface zoned, roughened by radial furrows, creamy with brownish tint, finely tomentose to subglabrous; context creamy, $0.5\text{ mm}-2.5\text{ mm}$, firm; tubes $2\text{ mm}-3\text{ mm}$ long; mouths irregular, angular, brownish cream in herbarium specimens, $2-3$ to the mm, dissepiments thin, breaking up; spores hyaline, $3\ \mu \times 5\ \mu$.

On dead stump, Knysna (720).

This fungus comes in 82 of Lloyd."

The type material in STE, collected in January, 1922, consists of small, seemingly more or less dependent brackets—the pilei having apparently grown downward from the point of attachment. They are subglabrous and resemble *P. rubidus*; the surface is buffy-brown with darker zones. The flesh, $0.5-2.5\text{ mm}$ thick is lignicolorous, the tubes are up to 3 mm long and the small pores, which are concolorous but show some evidence of bruising, are approximately $2-3$ per mm. The context of the pileus is seemingly dimitic although one would have expected it to be trimitic, comprising clamp-bearing generative hyphae and skeletal, $3.5-4.0\ \mu$ wide, which are subhyaline and solid; binding hyphae could not be demonstrated. Basidia are more or less ovate at first measuring $13.0 \times 7.2\ \mu$, and the spores, which are scanty and a little uncertain, are hyaline, elliptical, $8 \times 3\ \mu$.

The affinity of this fungus would seem to be with such species as *P. rubidus* Berk. and *P. albo-cervinus* Berk. etc. but these all have a trimitic hyphal structure.

Polyporus transvaalensis Van der Byl in S. Afr. J. Sci. **22**, 169, 1925.

"Plants annual, sessile, with a strong subiculum; pileus coriaceous, dimidiate, laterally connate, 2 cm to 5 cm by 0.7 cm by 0.4 cm; upper surface deep cream to tan-coloured, velvety tomentose to scabrous; context ochraceous, 3 mm to 4 mm thick, soft; tubes up to 2 mm long, mouths irregular, angular, 1 to 3 to the mm, dissepiments thin, brown; spores not found.

Collected by the author on rotten wood in the Haenertsburg distr., Transvaal (1475)."

The type material in STE consists of old sporophores in very poor condition which were collected in July, 1923. The fruitbodies are widely effused, and easily separable from the substrate, having curled away in places during drying. They are of very light weight and consist of small but elongated, reflexed brackets, measuring 2.0 cm from the margin to the point of attachment, with an obtuse margin. The surface, which is ochraceous-buff or darkish brown to grey brown, is slightly roughened with ropes of hyphae, evidently formed from the flattening of a weathered tomentum. On the effused part of the fructification the pores are open and elongate. The flesh, 3—4 mm thick, which is very soft and with the texture of cotton wool, is concolorous with the pileus. Anatomically the context appears to be dimitic consisting of clamp-bearing generative hyphae and skeletal, 4—5 μ diam., which are subhyaline with thickened walls although retaining a wide lumen. No hymenium is present and spores were not seen.

The affinities and systematic position of this fungus are not clear.

Polyporus trichiliae Van der Byl in S. Afr. J. Sci. **18**, 262, 1922.

"Plants annual, sessile, or effused reflexed; pileus dimidiate, conchate, densely imbricate, laterally connate, 0.5 cm to 3 cm by 1 cm to 2 cm by 0.1 cm to 0.9 cm; rigid and brittle when dry; surface creamy white to ochraceous, finely tomentose, rugulose; context 1 mm to 4 mm thick, creamy white, firm, corky; tubes 1 mm to 3 mm long; mouths minute, subrotund to irregular, 5 to 6 to the mm, edges thick becoming thin, chamois coloured to cinnamon; spores hyaline, smooth, ellipsoid, 5.5 μ to 7 μ by 3.7 μ ; hyphae hyaline, simple, 3.6 μ to 4 μ .

Distribution.—Known from a single collection on *Trichilia emetica* at Durban by the writer. (Type in Natal Herbarium, P. v. d. B., No. 897.)."

The material in STE, comprising Nos. 608, 572 and 129, all collected on the type host by Van der Byl at Durban, is *Xylodon subiculoides* (Lloyd) Reid. An unusual feature shown by collection No. 608 is that the brackets arise from a thick boss of tissue (—6 mm). Owing to the uniformity of these gatherings it seems fairly safe to assume that the type material also represents *X. subiculoides*.

See also under *Polyporus acaciae* Van der Byl.

Polyporus vicinus Lloyd in *Mycological Writings* 7, 1331, 1924 (Fig. 3055). (Fig. 23a-c.)

[non *P. vicinus* Bres. in *Ann. mycol.* 18, 35, 1920.].

"Pileus dimidiate, 3—4 inches in diameter 1,5—2 cm thick. (Plants sessile or effused-reflexed, at times imbricate, rarely substipitate; pileus dimidiate 10 cm $\times$ 7 cm—9 cm $\times$ 0,8 cm—2cm;) .Surface dull, white, or spotted with a reddish stain. (Surface white, at times spotted reddish black in older parts;). Context white, drying very hard and ligneous. (Context white, firm, corky, 0,6 cm thick;). Pores minute, isabelline, distinct from context as to color. Pore mouths adustus. (Tubes 1 mm—2 mm long, yellowish; mouth 4—5 to the mm; dissepiments thick, entire, greyish to dark;). Spores globose, large, 8—12 mic., hyaline, smooth. (spores hyaline, smooth, globose, 8 μ —12 μ .).

(Collected in Natal. 1153 and 1154).

This is another one of that confusing white *Apus* section. We would enter it in Section 89 although its relations are close to *Polyporus lignosus*. The globose spores and a suggestion of its pale color indicate its affinities."

According to Stevenson & Cash (1936) specimen 1153 is the type of the species. This gathering was studied in STE in part and consists of a large sporophore at least 10 cm wide, but it has become very enrolled in drying. The surface is creamy-white, minutely felty-pruinose (not tomentose), and smooth to undulating-knobly. One fruitbody has developed a red-brown almost waxy or horny cuticle and is only white-pruinose behind. The flesh is lignicolorous, and about 0,5 cm thick. The tubes, up to 1 cm deep behind are only 1 mm deep near the margin; the pores, about 5 per mm, scarcely visible to the naked eye, are greyish-ochre. Anatomically the flesh is trimitic, comprising dextrinoid skeletal hyphae, 4—5 μ diam., which are thick-walled, almost solid, glassy and destroyed in 10% KOH; and scanty binding hyphae, 2,0—2,5 μ diam., which are not densely coralloid but show more lax branching; generative hyphae were not demonstrated but will probably be found to bear clamp-connexions. The spores, 5,75—6,0 (—9,75) $\times$ 5,75—6,0 μ , which are scanty, vary in shape from globular to pip-shaped, and have a strongly dextrinoid wall. There are very abundant chlamydospores lining the tubes which are mostly globular but rarely obpyriform with a distinct apical papilla; they have a thickened dextrinoid wall and measure 9—13 μ diam. when globose or 11,75—19,2 $\times$ 9,3—11,2 μ when obpyriform.

Collection No. 1154 is probably conspecific but the fruitbody is reduced behind to a stipe-like base. This specimen has larger basidiospores in the hymenium which are ovate or pip-shaped, (6,2—) 8,0—9,5 $\times$ 5,0—7,0 μ , with a thickened, hyaline, dextrinoid wall. These spores would seem to belong to the fungus in question since they appear to be in groups of four.

This fungus is identical with *Fomes mesoleucus* Petch, which was described in 1925 from a single collection on a tree stump in December 1923 at Wariapolla, Ceylon. Another synonym is *Polyporus nigro-applanatus* Van der Byl described in November 1924, just a month after Lloyd published his *P. vicinus*. However it does not appear to belong in any of the known genera and hence the new genus *Vanderbylia* Reid is proposed to accommodate it.

***Vanderbylia* Reid, gen. nov.**

Sporophora sessilia, crassa, unguolata, dimidiata, effuso-reflexa raro basin versus indistincte substipitata. Contextus albus, vel lignicoloratus, in sicco durus vel ligneus, trimiticus; ex hyphis valde dextrinoideis compositus. Cystidia raro praesentia. Sporae globosae, ovatae vel guttiformes, muris crassis et valde dextrinoideis. Chlamydosporae plerumque praesentes.

TYPUS: *Vanderbylia vicina* (Van der Byl) Reid, comb. nov.

The type material of *F. mesoleucus* in K (Fig. 24 a-b) is very similar in all respects to the Natal collections, but the chlamydospores, which become almost black in Melzer's solution, appear to be more mature. They are alike in size and shape but appear to be slightly ornamented in a manner somewhat suggestive of *Ganoderma* spores.

In addition to *V. vicina* there is a second species belonging to the genus *Vanderbylia* which occurs in tropical Africa, i.e. *V. unguolata* Reid, sp. nov. which is described below.

***Vanderbylia unguolata* Reid, sp. nov. (Fig. 25 a-b.)**

Sporophora sessilia, crassa, primo dimidiata tandem unguolata, usque 37 cm lata, radialiter 22 cm et 9 cm crassa; superficies superior sub lente minute coacta, albida, in sicco ochraceo-bubalina, cuticula usque 2,5 mm crassa glabra atro-brunnea dura cornea tandem cooperta; cuticula vetustate fissurata et in areolas minutas omnino disrupta. Contextus usque 3 cm crassus, vel bubalinus vel cinnamomeo-brunneus. Tubuli stratosi, stratis usque duodecim; quoque strato usque 8 mm crasso. Pori 4—5 per mm, rotundati, ochraceo-bubalini. Hypharum systema trimiticum; hyphae skeletales, 2,5—3,5 μ diam., dextrinoideae, muris pallide brunneis, crassiusculis sed lumine distincto instructae; hyphae ligantes, 1,5—2,0 μ diam., dextrinoideae, laxae ramosae; hyphae generatoriae non visae. Basidiosporae vel chlamydosporae abundantes, 5,0—6,0 (—7,5) μ diam., globosae vel ovoideae, pallide brunneae, dextrinoideae, poris germinatoriis 2 vel usque 4 instructae.

TYPUS: On *Pterocarpus angolensis*, Nachingwea, Tanzania, coll. B. Boaler, 5 Sept. 1962.

Sporophores sessile, at first dimidiate, becoming unguulate and then up to 37 cm wide, 22 cm from point of attachment to the acute or very thick and obtuse margin, and up to 9 cm thick; upper surface very minutely felty under a lens, whitish when fresh, ochraceous-buff when dried, but soon developing a hard,

dull blackish-brown, glabrous, horny cuticular layer from behind, which quickly envelops the entire surface, except sometimes for the narrow, actively growing marginal zone. The cuticle is often very thick, up to 2.5 mm in old specimens, but it is then frequently conspicuously fissured and at the same time completely disrupted into small areolae. Old specimens are also concentrically sulcate. The context, up to 3 cm thick, varies in colour from buff to pale cinnamon-brown. The hymenophore is ochraceous-buff and may be poroid to the extreme edge or there may be a broad sterile marginal zone devoid of pores; tubes strongly stratified with up to 12 strata, each stratum being up to 8 mm thick; pores 4—5 per mm, rounded, with thick dissepiments. Hyphal structure of the context trimitic, consisting of long, unbranched dextrinoid skeletal hyphae, 2.5—3.5 μ wide, which taper to a very long, narrow, hyaline, thin-walled apex, but otherwise with very pale brownish thickened walls, but retaining a fairly wide, septate lumen; and scanty dextrinoid binding hyphae, 1.5—2.0 μ wide, which exhibit rather lax branching; generative hyphae not actually seen. In the tubes the hyphae are more intricately branched, difficult to separate, and mostly about 2 μ wide. Hymenium lacking although there are abundant pale brownish, dextrinoid spores, 5.0—6.0 (—7.5) μ diam., which may be chlamydospores lining the walls of the tubes. They are thick-walled, vary in shape from globose to ovoid and have at least 2 and sometimes up to 4 germ-pores which appear as bright hyaline spots.

Collections examined from: Tanzania: on living *Pterocarpus angolensis*, 3 m above the ground, Sakililo, Rukwa Rift Valley, coll. S.B. Boaler [Gibson No. 803 and 803D], 15 Dec. 1961; On living *P. angolensis*, Iringa Road, Chimala, near Mbeya, coll. S. B. Boaler (No. 1059), March 1963; On *P. angolensis*, 50 cm above the ground, Nachingwea, coll. S. B. Boaler, 5 Sept. 1962 [TYPUS]. Zambia: on *Afrormosia angolensis*, Mpata Gorge, coll. D. B. Fanshawe (No. 46), 6 Sept. 1963; On *Afrormosia*, Kabompo, coll. D. B. Fanshawe (No. 76), 10 Sept. 1964; On *P. angolensis*, Luapula Valley, coll. J. Mackenzie, 1963. Malawi: On *A. angolensis*, Njuli Tea Estate, Cholo, without details of collector, No. 1568.

Judged from available data *V. unguolata* differs from *V. vicina* in having more robust fruitbodies with a very thick cuticle, buff to pale cinnamon-brown flesh, narrower skeletal hyphae which retain a wide lumen and take longer to show the dextrinoid reaction, and different chlamydospores with 2—4 germ-pores. In addition *V. unguolata* has a more tropical distribution and is seemingly restricted to hosts belonging to the *Leguminosae*.

Other species which belong to the genus *Vanderbylia* are *V. hornoderma* (Mont.) Reid, comb. nov. [*Polyporus hornodermus* Mont. in Annls Sci. nat. Series 4, 5, 368, 1856]; *V. latissima* (Bres.) Reid, comb. nov. [*Fomes latissimus* Bres. in Annls mycol. 8, 588, 1910]; and *V. fraxinea* (Bull. ex Fr.) Reid, comb. nov. [*Polyporus fraxineus* Bull. ex Fr. in Systema Mycologicum 1, 374, 1821].

V. hornoderma is easily recognized by the absence of encrusted cystidia in the tubes and by its very characteristic elongated narrow pip-shaped, clavate, bottle-shaped or flask-shaped dextrinoid spores, $6.0-8.0 \times 3.5-4.0 \mu$, which are not seemingly apiculate and have a distinct pore at the narrow end and a smaller one at the broad end; these pores show as bright hyaline spots in certain views.

Lowe (1957) used the name *Fomes ligneus* (Berk.) Cooke for this fungus and he was followed by Wright (1964) who noticed the dextrinoid reaction of both spores and hyphae and transferred the species to *Poria* s. str. as *Poria lignea* (Berk.) Wright. However, examination of the type of *F. ligneus* in K has shown that although sterile, it is a quite distinct species unrelated to *F. hornodermus*, since it has non-dextrinoid hyphae. Lowe (loc. cit.) also kept *F. sulcatus* (Cooke) Cooke separate from *F. ligneus* sensu Lowe [i.e. *F. hornodermus*] on the basis that it had context hyphae mostly $2-4 \mu$ diam., whereas in *F. ligneus* sensu Lowe they are $4-8 \mu$. In fact the context hyphae of the type specimen of *F. sulcatus* are up to $6 (-7) \mu$ diam. Hence *F. sulcatus* is best relegated to synonymy under *V. hornoderma*.

V. latissima (Fig. 27 a-b) is extremely similar to the previous species, differing only in the narrower hyphae, $2.5-3.5 \mu$ wide, and presence of thick-walled clavate or obpyriform, apically encrusted, dextrinoid cystidia. It is found in tropical Africa, India, and the Pacific Islands (Java, New Guinea)—many of the collections having been referred to *V. hornoderma*. Just how reliable the presence or absence of cystidia is as a taxonomic character remains to be seen. However of 5 South American gatherings of *V. hornoderma* none was found to have cystidia whereas out of 10 collections so-named from Africa, India and Malaysia, 7 showed cystidia in varying abundance. It is not clear whether the remaining 3 gatherings represent true *V. hornoderma* or whether they represent *V. latissima* in which cystidia are so scanty as to have escaped detection.

V. fraxinea (Fig. 26 a-b), which occurs in Europe and North America, has thick-walled, strongly dextrinoid, oval or pyriform spores, measuring $6.0-6.75 \times 4.2-5.75 \mu$, with an apical thin-walled area or pore, at least in some of the spores. These spores are basidiospores since they have a definite apiculus and have been seen attached to basidia. There is considerable uncertainty regarding the specific name of this species, see Donk (1971).

Another fungus which may belong in *Vanderbylia* is *Fomes mundulus* Wakef. from Rhodesia, since this has a dark blackish, some what rimose crust and strongly stratified tubes. Further, the flesh is largely composed of dextrinoid hyphae but the spores although broadly elliptical or ovate and dextrinoid are distinctly truncate at one end. *Heterobasidion annosum* (Fr.) Bref. also has dextrinoid hyphae but the minutely roughened, very broadly elliptical or ovate spores are non-dextrinoid.

Trametes albotexta Lloyd in Mycological Writings 5, Mycological Notes No. 44 p. 614, 1916. [Fig. 868]. (Fig. 19.)

"Pileus sessile, 2—3 × 4—5 inches, an inch thick, surface reddish brown, dull, matt, soft. (Pileus sessile, dimidiate, 8 cm to 10 cm by 5 cm by 1,4 cm to 4 cm; surface reddish-brown, soft to hard, rugulose, tomentose to subglabrous, smooth or scabrid to touch;) Context reddish brown, thin, soft. (context 0,4 cm to 0,7 cm, firm, tough, corky, reddish-brown;). Pores rigid, small, round, an inch long. Pore tissue white, contrasting with the brown hymenium so that a section is variegated. (tubes 0,5 mm to 1,5 mm long, tissue white with reddish-brown hymenium; mouths subrotund to angular, 2 to 3 to mm, edges entire or produced into teeth, white changing to yellowish and dark brown;). Cystidia none. Spores pale brown, small, ellipitcal-subglobose, 3—4 × 4—5. (Spores pale brown in mass, subglobose 3,7 μ by 5 μ; hyphae, 4 μ to 5 μ.).

The coloration of the surface, pore surface and context is reddish brown, the tissue of the pores white. I know of no other *Trametes* or polyporoid with this peculiar color pore contrast. The pale colored spores might be the basis for a "new genus", but I think that would be "inutile".

Van der Byl added "*Distribution*. On dead *Podocarpus* sp. in Hlatikulu Forest (Type in Natal Herbarium, No. 181). Collected also by Miss A. V. Duthie.

The surface and context colour are peculiar and would aid in the recognition."

The specimen in STE bears the following data "On *Podocarpus* sp., Eastern Cape, No. 312", but is clearly conspecific with the type judged from the description. It has a very dark surface with alternating dark brown tomentose zones and black glabrous bands giving the brackets very much the appearance of *Ischnoderma resinosum* (Fr.) Karst. The flesh, 4—8 mm thick, is lignicolorous; the pores are brownish and the tubes are lined with a brownish hymenium. Anatomically the flesh is monomitic comprising glassy generative hyphae. up to 8 μ diam., with clamp-connexions at the septa; these hyphae have a central thread of contracted contents when examined in 10% KOH. There are also coloured conducting organs with brown contents; these are scanty and were seen mostly near the cuticle. The hyphae of the surface tomentum are brown. The spores, 4,2—6,0 × 2,5—3,0 μ, are hyaline, elliptical and appear glassy and refractive.

This species appears to belong in the genus *Ischnoderma* Karst. and is hereby transferred to this genus as *Ischnoderma albotextus* (Lloyd) Reid, comb. nov. It differs from *I. resinosum* in the broader elliptical, non-allantoid spores.

*While this paper was in press Ryvarden published an article (*Norweg. J. Bot.* 19: 141—143, 1972) in which he discussed the generic name *Perenniporia* Murr. and he would clearly have included in that genus those species of *Vanderbylia* listed above. What he has not demonstrated is whether Murrill's interpretation of *Poria unita* was the currently accepted one. This is essential since *P. unita* has been selected as the type species of *Perenniporia*. Interpretation of this genus must therefore depend on Murrill's concept of *P. unita* irrespective of how *P. unita* is itself typified. I hope to return to this question in the sequel to this paper.

It should be noted that Doidge (1950) cites a number of additional collections on various hosts.

Trametes griseo-lilacina Van der Byl in S. Afr. J. Sci. **18**, 283, 1922. (Fig. 20.)

"Plants annual, sessile; pileus coriaceous to corky, applanate, imbricate, dimidiate to laterally extended, 3 cm to 10 cm by 2,5 cm to 4 cm by 4 cm to 0,8 cm; surface concentrically sulcate, tomentose to glabrous, fasciculate setose, rugulose, scrupose, grey to greyish fawn; margin acute, tomentose on upper surface; context corky, firm, fibrous, lilac-mauve to mouse coloured, 3 mm to 4 mm; tubes 0,5 mm to 2,5 mm long, lighter than context; mouths unequal, irregular, round to elongated and angular, 2 to 3 to the mm; edges thick, entire, concolorous, lilac-mauve; spores hyaline, smooth, oblong, $3,7 \mu$ by $7,5 \mu$; hyphae simple, $3,5 \mu$ to 6μ .

Distribution.—Single collection by Geo. Hobbs on railway sleeper at Illovo River, Natal. (Type in Natal Herbarium, No. 921.)

The context colour and colour of pore mouths is peculiar and should aid in the identification of the fungus. The fungus is evidently related to the Australian *Trametes lilacino-gilva* (Berk.) Lloyd, but with rougher surface and irregular pore mouths."

The specimen at STE, also collected on a railway sleeper, at Durban bears the No. 1060 [yet another specimen on a railway sleeper from Durban bears the No. 150]. Collection No. 1060 has the context of the pileus seemingly rudimentarily trimitic. The generative hyphae, $2,5-3,0 \mu$, are hyaline and bear clamp-connections; the skeletal, $3,5-7,0 \mu$, have thickened red-brown walls but retain a wide lumen. It is difficult to be certain whether there are true binding hyphae but there are solid, kinked, hyaline, laxly and sparingly branched hyphae present. The spores are hyaline, elliptical, $6,0-7,75 \times 3,0 \mu$.

Trametes ochrolignea Lloyd in Mycological Writings **5**, Letter No. 63, p. 10, 1916.

"(Plant forms a hard flat, woody and unseparable mass, 2 mm thick, on the wood of which it grows, the periphery of this mass is continued into the pilei or the pilei develop separately from it;). Pileus woody, sessile, 4 to 6 inches in diameter, an inch thick (Pilei subcircular 6 cm to 10 cm diam., by 0,7 cm to 2 cm thick;). Surface uneven, not zoned, reddish brown [Roods Brown, Ridgway], minutely pubescent. (Surface uneven, tuberculate, reddish brown, more yellow towards margin, tomentose, with a few concentric furrows;). Context hard, woody, yellow (Context 3 mm to 8 mm thick, corky to hard and woody, yellow, shining;). Pores round, or elongated, medium, somewhat irregular. (Tubes about 1 mm long; mouths round to elongated, irregular, 2 to 3 to the mm; edges thick or thin, somewhat lacerate, yellow;). Spores 3×6 , cylindrical hyaline, smooth. (Spores hyaline, smooth, $3,7 \mu$ by 7μ ; hyphae 3μ by 7μ diam.).

Trametes Zimmermanni, a species named in MSS at Berlin, and *Trametes ochro-flava* of Brazil, which is really a *Fomes*, are the only other species known to me with yellow context. Although the hymenial configuration is so different, with same texture, context color and spores, *Daedalea Dregeana*, *Daedalea Eatonii* and *Tremetes ochrolignea* are for me variations of the same species. Zones of annual growth and indistinct pore strata are seen in *Trametes ochrolignea* so that it is really a *Fomes*."

Van der Byl added the following data:—"Distribution.—Found at Durban, Natal, on rotten log. Distinguished from *P. occidentalis* by its habit of growth, more tuberculate surface and context in older part and part above the substratum being extremely hard and woody. (Cotype in Natal Herbarium, No. 226)."

The specimen in STE, although from Durban, bears the number 106, and whilst not the type of the species, is clearly conspecific with it. This specimen is merely a thick woody form of *Coriopsis (Polystictus) occidentalis* (Kl.) Murr.

Trametes salebrosa Van der Byl in S. Afr. J. Sci. **21**, 313, 1924. (Fig. 38.)

"Pileus perennial, sessile, woody, decurrent at attachment, dimidiate, 8 cm × 4 cm × 0.7 cm—2 cm; surface azonate, rough with stiff projections, greyish; context firm, dark reddish brown, shining and velvety in appearance, 3 mm—7 mm thick, tubes 1 mm or less long, mouths subrotund to angular, 3—4 to the mm; setae absent.

Collected at Knysna (1063).

This fungus resembles *Polyporus gilvus* externally, but has darker context and no setae."

The type material, collected in January 1922, is represented in STE by half a sporophore measuring 5.5 cm in length and 4.5 cm from the point of attachment to the margin. The upper surface is dark brown and scrupose as in *Phellinus scruposus*; the flesh, 1 cm thick behind, is rich brown and dark silky-fibrillose; the tubes are 1 cm long and the pores are 2—3 per mm. Anatomically the flesh is trimitic, comprising brown skeletal hyphae, —8 μ diam., with very thick walls but retaining a wide septate lumen, and coralloid binding hyphae, 2—3 μ diam., which are also thick-walled with a distinct septate lumen. These binding hyphae, which form dense clumps, arise from hyphae very like the skeletal except that they bear clamp-connexions. No hymenium or spores were seen.

This fungus is closely related to *Coriopsis badia* (Berk.) Murr. and *Coriopsis strigata* (Berk.) Reid and belongs in the genus *Coriopsis* Murr. It is hereby so transferred as *Coriopsis salebrosa* (Van der Byl) Reid, comb. nov.

Trametes subflava Lloyd in Mycological Writings **5**; Letter No. 66, p. 8, 1917. (Figs. 21 a—b; 39.)

"Entire plant (including context) unicolorous, about maize yellow with pore mouths somewhat darker, ungulate, sessile (Pileus sessile, ungulate, sub-

triquetrous, 10 cm by 14 cm by 8 cm; surface soft, velvety-tomentose, light yellow). Context light and stupose (context 0.5 cm to 2 cm thick, yellow, soft, tough, tow-like; (Pores very minute, little developed. (tubes 1 mm or less long; mouths subrotund 4 to 6 to the mm; edges thin, entire, darker yellow than the context shining;)) Cystidia with capitate, rough heads. Spores (if correctly seen) globose, 4—5 mic. (Spores hyaline, globose, 4 μ diam.).

We received this before from Mr. Van der Byl (No. 79) and at the time referred it, with doubt to *Fomes connatus*, which is somewhat similar in color and has the same spores and peculiar cystidia. An additional collection, however, which is the same exactly as the first, and which differs from *Fomes connatus* in manner of growth, and particularly in its soft, punky context, convinces us that we were wrong, and the only thing to do is to name it *Trametes*, where it belongs.

It reminds one of *Fomes floccosus*, of Ceylon (which is perhaps a better *Trametes*) as to light context, and of *Fomes connatus* as to color, cystidia, and spores."

Van der Byl added the following data "*Distribution*.—Found on live *Celtis kraussiana* by J. D. Keet in Eastern Cape Forest Conservancy. (Cotype in Natal Herbarium, No. 388.)"

The specimen examined in STE bears the following data "Eastern Cape Province, No. 267". However, there is again some confusion involving the numbering of the specimens. Doidge (1950) cited No. 267 under *T. subflava* with the additional information "on *Celtis kraussiana* Bernh., on living trees, Eastern Cape, Keet (v. d. Byl 267)." This ties up with Van der Byl's published data quoted above, with the exception that he quoted the number of this specimen in the Natal Museum as No. 388. In any event specimen 267 in STE is clearly conspecific with *T. subflava* as described by Lloyd.

It consists of part of a large ungulate, light-weight sporophore measuring 10 cm in thickness and 10 cm in width at the base, across the hymenophore. The material is now entirely buff-coloured, but the minute pores appear either brown or buff according to the incidence of the light which causes them to glance. Anatomically the flesh is monomitic consisting of generative hyphae, 2.5—4.0 μ wide, with distinct, slightly thickened pale straw-coloured walls. These hyphae are septate, but devoid of clamp-connexions. In the hymenium there are small, apically encrusted, capitate cystidia, 18.75 μ long, 6—8 μ wide (including the encrustation). The spores, 2.5—3.2 μ diam., or 3.2—4.0 $\times$ 2.2—3.2 μ , are thin-walled, hyaline and vary in shape from globose to ovate to very broadly elliptical.

This fungus belongs in the genus *Oxyporus* (Bourd. & Galz.) Donk and is hereby transferred to this genus as *Oxyporus subflavus* (Lloyd) Reid, comb. nov.

Trametes tomentosa Van der Byl in S. Afr. J. Sci. 18, 285, 1922.

"Plants effused-reflexed, annual; pileus applanate, coriaceous 9 cm by 7 cm by 0.1 cm to 0.4 cm; surface with a few faint furrows, rugulose, covered with a soft

cinnamon brown tomentum; margin thin, undulate; context 0.5 mm to 2 mm thick, azonate, corky, shining, straw yellow; tubes 0.5 mm to 1.5 mm long, elongated on decurrent part, concolorous with context; mouths subrotund to irregular, 2 to 3 to the mm; edges thick towards margin, thin in older parts, entire to somewhat lacerate, yellow-buff; hyphae $4\ \mu$ to $5\ \mu$ diam.

Distribution.—Found on dead logs at Durban, Natal, by the writer.

The plant is in its context colour and colour of pore mouths close to *P. occidentalis*, Kl., from which it differs in the finer tomentum. The hairs are longer and finer and the surface has a feeling of plush. (Type in Natal Herbarium, P. v. d. B., No. 836.)

There is a specimen so named from Durban by Van der Byl, in STE, bearing the No. 707. This agrees with the original diagnosis and represents a large, thin, flaccid form of *Corioloropsis (Polystictus) occidentalis* (Kl.) Murr.

Trametes varians Van der Byl in S. Afr. J. Sci. **18**, 281–282, 1922. (Fig. 22.)

“Plants effused-reflexed to largely resupinate; pileus corky, rigid, dimidiate, imbricate, at times conchate, 2 cm to 4 cm by 0.7 cm to 2 cm by 0.5 cm to 1 cm; surface azonate, minutely pubescent, frequently somewhat tuberculate, at times rugulose and scabrid, creamy white becoming ochraceous to somewhat fuliginous; margin acute, cream coloured or fuliginous; context 1 mm to 2 mm thick, corky, creamy white; tubes 1.5 mm long, discoloured within; mouths angular to elongated, irregular, approximating 4 to the mm; edges entire, creamy white to greyish and greenish drab; hyphae $7.24\ \mu$ diam.

Distribution.—Recorded from Eastern Cape Forest Conservancy. (Type in Natal Herbarium, No. 151.)

Differs from *T. glabrescens* in habit, surface and pore-characters.”

There is in STE a specimen from Eastern Cape Province bearing the No. 527. This comprises very nondescript, thin, effused, slightly pileate fruitbodies. The pileate portion, 0.5–1.0 mm, from the substrate to the margin, has a minutely tomentose, uneven or slightly scrupose surface, which is entirely greyish-buff. The pores, 2–3 per mm, are angular with thin dissepiments. Anatomically the context, which contains a fair amount of oily substance as seen when mounted in 10% KOH, comprises thin-walled clamp-bearing generative hyphae and glassy skeletal, $5\ \mu$ wide, which look as though they may have been affected by the KOH solution. No binding hyphae were seen. The spores, $4.0\text{--}5.0 \times 1.75\text{--}2.0\ \mu$, were thin-walled, hyaline and elliptical.

This fungus appears to represent young fructifications of a *Coriolus* Quél., which have not yet developed any binding hyphae.

HYDNACEAE

Hydnum longosporinum Lloyd *apud* Van der Byl in S. Afr. J. Sci. **25**, 185, 1928. [First published by Lloyd in Mycological Writings 7, 1186, 1923 as a nomen nudum.]. (Fig. 32 a–c.)

"Pileus sessile, dimidiate, imbricate, firm and rigid when dry, 3—4 cm long, 1—2 cm broad; surface maize yellow, velvety tomentose, tuberculate, indistinctly sulcate; context maize yellow, 1 mm thick; teeth dark fawn, slender, up to 5 mm long, 250—440 μ diam. at base. On old wood. Exact locality unknown but probably Knysna.

Lloyd published the name of this fungus in 1923, but a description has, to my knowledge, thus far not been published."

This name was introduced as a nomen nudum by Lloyd in 1923, in a list of determinations of fungi sent to him for naming by Van der Byl. However, according to Stevenson & Cash (1936) there is no material of *H. longosporosum* in the Lloyd Herbarium and it therefore seems probable that the collection in STE bearing the following data—Knysna, 1922. Type 775.—represents the only remaining portion of the original gathering. It consists of small, imbricate brackets with a smooth, tomentose surface. The hymenophore is densely spinous; the spines being up to 6 mm long, thin, pointed (as in *Steccherinum* spp.) and fairly dark brown. Anatomically the spines are dimitic, consisting of long, thick-walled, almost solid skeletal hyphae, 4.5 μ wide, but with a distinct lumen expanding toward the slightly enlarged apex, which is for the most part thin-walled and sometimes secondarily septate; and thin-walled, clamp-bearing generative hyphae, 2.5 μ wide. There are no encrusted cystidia, although it is just possible that there may be some thick-walled, poorly differentiated elements in the hymenium. Basidia are produced in tufts along the generative hyphae but spores are very scanty. They are, 3.5 $\times$ 1.5 μ , small, hyaline and elliptical, but it is not absolutely certain that these belong to the fungus in question.

This fungus, illustrated by Van der Byl (1934), reminds one of *Steccherinum rawakense* (Pers. *apud* Gaud.) Banker, which has been very fully described by Maas Geesteranus (1964).

Hydnum pulchrum Lloyd in Mycological Writings 6, 918, 1920 as *H. pulcher* (Fig. 1641).

"The section of *Hydnum* with colored spores is rare. No species occurs in Europe or the States and this is the fifth one that has come to my notice.

(Fruitbody sessile, pileate). Pileus dimidiate, thin, probably white when fresh, but reddish when dried (Pileus dimidiate, fleshy-leathery, thin, flexible, 5 $\times$ 9 cm, upper surface glabrous, sandy-, red-, or yellowish-brown in dried specimens—apparently white in fresh material. Flesh pale or colourless, 1—2 mm thick.). Teeth short, about 1 mm, blunt, dark reddish-brown when dried. (Spines about 1 mm long, blunt, sandy-brown to dark reddish-brown in dried specimens, apparently somewhat gelatinous; trama pale, hymenium much darker.) Cystidia none. Spores abundant, 3.5 $\times$ 4.5, smooth, colored. (Spores smooth, coloured, 3—4 $\times$ 4—6 μ .)

There is another species of this section in South Africa (cfr. Myc. Notes, p. 597) which differs much from this. Excepting in the colored spores this reminds one of *Hydnum pulcherrimum*. A section shows the teeth of a subgelatinous nature, a feature unknown to me in other *Hydnums*. The trama is pale, compact and the hymenium much darker color."

Van der Byl added that it grew "on dead stump; Durban, Natal (J. B. Leslie)."

According to Stevenson & Cash (1936) the type collection is that bearing Van der Byl's number 881. The specimen so-named in STE, collected by J. B. Leslie at Durban, bears the No. 534. It is in poor condition, consisting of a number of pilei. The context is monomitic, comprising thin-walled, mostly collapsed hyphae, about $6\ \mu$ wide, which seemingly lack clamp-connexions. The spores, $4.5-6.0 \times 3.0-3.5\ \mu$, are yellowish-brown and have a distinct wall.

This fungus belongs in the genus *Gyrodontium* Pat. It should be noted that Maas Geesteranus (1966) has published a full account of the type material preserved in the Lloyd Herbarium, and is of the opinion that it is identical with *Gyrodontium versicolor* (Berk. & Br.) Maas Geesteranus.

Odontia knysnana Van der Byl in *Annale Univ. Stellenbosch* 12, A1, 9, 1934. (Fig. 29.)

"Fruitbody resupinate, adnate, thin, becoming cream, confluent $1-3 \times 3-10$ mm; margin byssoid. Context hyaline, $120-220\ \mu$ thick; hyphae $3-4\ \mu$ thick, thin-walled with clamp-connexions, smooth or ornamented with crystals, running parallel to the upper surface, branched, lax, dense and indistinct in the sybhyemenium. Teeth short, granular, $6-8$ to the mm, tips of the teeth fimbriate (fimbriae only visible with the help of a hand lens.) Spores colourless, $3 \times 5-6\ \mu$. Cystidia about $4\ \mu$ thick.

On rotten wood. Knysna." [From the Afrikaans].

The material in STE, which would seem to be the type collection, was gathered at Knysna, January 1924, and bears the No. 1332. It consists of small-scattered, resupinate, creamy-white patches with a byssoid, but non-rhizomorphic margin. The teeth are short, crowded and almost Grandinioid. Anatomically the context is monomitic, comprising clamp-bearing generative hyphae, $3\ \mu$ wide, with thickened walls although retaining a wide lumen; the clamp-connexions are small and inconspicuous. Many of the hyphae in the axes of the teeth are covered with amorphous granular material. In the hymenium there are long pointed cystidioles, up to $40\ \mu$ in length, in which the basal portion may become slightly thick-walled. The spores, $5-6 \times 3\ \mu$, are rather broadly elliptical.

This fungus belongs in the genus *Hyphodontia* J. Erikss. and is very reminiscent of *H. crustosa* (Pers. ex Fr.) J. Erikss. It is hereby transferred to this genus as *Hyphodontia knysnana* (Van der Byl) Reid, comb. nov.

CLAVARIACEAE

Clavaria durbana Van der Byl in S. Afr. J. Sci. **29**, 322. 1932. (Fig. 30.)

"Fruitbodies caespitose, branched, small, flesh-coloured, 2,5 cm high, 1,5 cm broad. Stalk 2 mm thick, 6 mm long. Branches crowded, cylindrical or flattened. Spores oblong, rough, $3 \times 6 \mu$, very pale ochre-coloured to almost hyaline.

On dead stump, Durban, Natal, by the writer.

In shape and colour this species agrees with *C. gracilis*, Pers., but it differs in the much rougher spores." [From the Afrikaans].

The material in STE, "collected on a stump, Durban, No. 661" consists of a tufted fruitbody 2 cm high and 1,7 cm wide, with densely crowded branches arising from a short main trunk, 0,8 cm high and 0,2 cm wide. The entire plant is now ochraceous; the branches are flattened at the axils but not conspicuously so elsewhere. Anatomically the flesh is monomitic, consisting of thin-walled, clamp-bearing generative hyphae, $2,0-2,5 \mu$ diam. The spores, $4,5-5,5 \times 3,0-3,5 \mu$, are thin-walled, hyaline or very faintly tinted, and elliptical.

In his monograph of "Clavaria and allied Genera" Corner (1950) transferred Van der Byl's fungus to the genus *Ramaria* S. F. Gray as *Ramaria durbana* (Van der Byl) Corner without seemingly having studied authentic material, yet at the same time he noted "I think it may be *Scytinopogon*". In fact it would appear to be identical with *S. angulisporeus* (Pat.) Corner, which is a common tropical species.

LACHNOCLADIACEAE

Lachnocladium cristatum Lloyd in Mycological Writings **6**, 890, 1919. (Fig. 1547). (Fig. 33 a-c.)

"Stems branched from the base and cristated at the summit. Surface pubescent to the eye. Texture rough. Colour pale ochraceous. Hairs under the microscope hyaline, sharp, smooth, projecting about 20 mic. Spores abundant, hyaline, subglobose but irregular, 3-4 mic. I have compared all my photographs of *Lachnocladium* and find none to correspond but of course it may have a name as *Clavaria*."

The material in STE is part of the type collection, which was from Forest Hall, Knysna, coll. A. V. Duthie. The fruitbodies have the context of the main branches formed of stellate elements which are basically 4-rayed although some may be 5-rayed or have one of the rays forked near the tip. These stellate bodies have slightly thickened, pale yellowish-brown walls, and measure approximately $63-88 \mu$ diam. at their widest point. Toward the hymenium they are smaller and less regular in shape, measuring $22,2-35,0 \mu$ diam. In the hymenium itself there are large conspicuous gloeocystidia with oily contents; spores are abundant, $3,0-3,2 \times 2,2-3,0 \mu$, thin-walled, hyaline, varying in shape from ovate to very broadly elliptical.

This fungus is correctly assigned to the genus *Lachnocladium* Lév.

TREMELLALES

DACRYMYCETACEAE

Dacrymyces australis Lloyd in Mycological Writings 6, 924, 1920. (Fig. 34 *a b*.)

"(Fruitbody jelly-like, up to 2 cm high). Cerebriform with gyrose lobes. Color clear egg yellow (dried fruitbody dark with resinous appearance). Basidia forked. Spores 7×20 ($16-20 \times 7-8 \mu$), slightly curved, mostly septate (divided into 2-9 cells). It is so close to *Dacryomyces digressus* (Cfr. Myc. Notes p. 620) that we hesitate to name it otherwise, and yet when soaked out it is a very different plant. This specimen has a yellow fruiting surface borne on a pale, almost white base which may have been shielded from the light in growing. We can not say that this is a constant character, but if normal the plant could well be named *Tremella bicoloris*. This is the third species of *Dacryomyces* that simulates a *Tremella* that we know."

According to Stevenson & Cash (1936) the type number of Van der Byl's specimen which he sent to Lloyd and upon which the latter author based the species was No. 816. However when Van der Byl subsequently discussed the species in 1923 he cited only two collections Nos. 595 and 627, both from Pietermaritzburg. The material examined in STE bears the No. 595, and consists of a parchment-like horny film which is flattened in one plane but gyrose-folded at the apex. The flesh is formed of hyphae, 2.5μ thick, which lack clamp-connexions. The spores, $19.0-20.8 \times 5.0-6.0 \mu$, are elongated, narrowly elliptical to slightly curved and become 7-septate at maturity; the septa being rather thick; germination appears to be by the production of numerous germ-tubes.

McNabb (in litt.) has relegated *D. australis* to synonymy under *D. palmatus* (Schw.) Bres. after a study of the type specimen in the Lloyd Herbarium.

Guepinia agariciformis Lloyd *apud* Van der Byl in Annale Univ. Stellenbosch 1, 4, 1923. [First published by Lloyd in Mycological Writings 7, 1186, 1923 as a nomen nudum.] (Fig. 31 *a-b*.)

"Plants growing in dense groups; fruitbodies jelly-like, pale yellow, spatulate-funnelshaped, 1 cm high; hymenium distinctly folded with the folds resembling gills; spores colourless, curved, 2-celled, $19 \times 4 \mu$."

On old wood, Pietermaritzburg (770). *G. agariciformis* is probably only an unusual growth-form of *G. spathularia*; the main difference is in the hymenium"

The material in STE, part of the original gathering No. 770, probably formed the basis of Van der Byl's description of the species and hence should be regarded as the holotype of *G. agariciformis*. It consists of expanded-flabellate fruitbodies, up to 1 cm high, with the sterile upper surface covered by a buff-coloured tomentum. The lower hymenial surface is orange, ornamented with gill-like folds which persist when the fructification is soaked up in water. The hyphae, 2.5μ wide, have a firm, distinct wall and 'H'-connexions are frequent, but clamps are lacking. The hymenium comprises basidia up to 29μ long, and very

narrow septate paraphyses; spores, $6.5-9.5 \times 2.75-3.0 \mu$, are thin-walled, elliptical, and become tardily 1-septate. [Van der Byl's spore measurements clearly involve an orthographic error and should read $9 \times 4 \mu$ instead of $19 \times 4 \mu$.]

McNabb (in litt.) has relegated *G. agariciformis* to synonymy under *Dacryopinax* (*Guepinia*) *spathularia* (Schw.) Martin and undoubtedly it is little more than a growth form of the latter species. Nevertheless, it is rather striking in the field and is perhaps worthy of recognition with the status of a form ie. as *Dacryopinax spathularia* forma *agariciformis* (Lloyd apud Van der Byl) Reid, comb. nov.

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**STUDIES IN THE GENERA OF THE *DIOSMEAE* (RUTACEAE): 1.
AGATHOSMA ROSMARINIFOLIA (BARTL.) WILLIAMS COMB. NOV.**

ION WILLIAMS

(*Compton Herbarium, Kirstenbosch*)

ABSTRACT

Examination of fresh material reveals that *Acmadenia rosmarinifolia* Bartl. should be transferred to the genus *Agathosma*.

UITTREKSEL

STUDIES VAN DIE GENERA VAN *DIOSMEAE* (RUTACEAE): 1. *AGATHOSMA ROSMARINIFOLIA* (BARTL.) WILLIAMS COMB. NOV.

'n Ondersoek van vars monsters toon dat *Acmadenia rosmarinifolia* aan die geslag *Agathosma* toegevoeg moet word.

DISCUSSION

The recent collection of fresh material in the Fernkloof Nature Reserve (Williams 1652 & 1736) has made possible a more detailed examination of this species. Ecklon & Zeyher (1835), one of whom was the first to gather this plant, wrongly identified it with *Barosma foetidissima* Bartl. & Wendl. It was found "Inter frutices et saxa (altit. IV) prope villas Swart et Marais ad montem Babylons Toorensberg (Caledon). Aug." Bartling (1843), citing *Barosma foetidissima* sensu Eckl. & Zeyh., placed this plant in the genus *Acmadenia* and named it *Acmadenia rosmarinifolia*. Bartling's closing remarks translated into English read "A species both unusual in appearance in this genus and truly singular in the internal floral parts, not in the least like any of its cogeners". His excellent description in *Linnaea* could scarcely be improved upon but he did, unfortunately, fail to observe that the ovary was three-chambered which fact alone points to the genus *Agathosma*. Other characters which definitely assign a species to the genus *Agathosma* are, firstly, the style should approximately equal the petals and, secondly the stigma should be simple. In this species the style equals the stamens in length but does not quite equal the petals. However by no means does it become as long as in *Macrostylis* nor remain as short as in *Acmadenia*. The stigma would appear to be capitellate rather than simple, but the difference is so slight as to be of no significance. In all other characters this species falls into *Agathosma*. The most obvious are:—flowers are aggregated in many-flowered heads; each flower is pedicellate with

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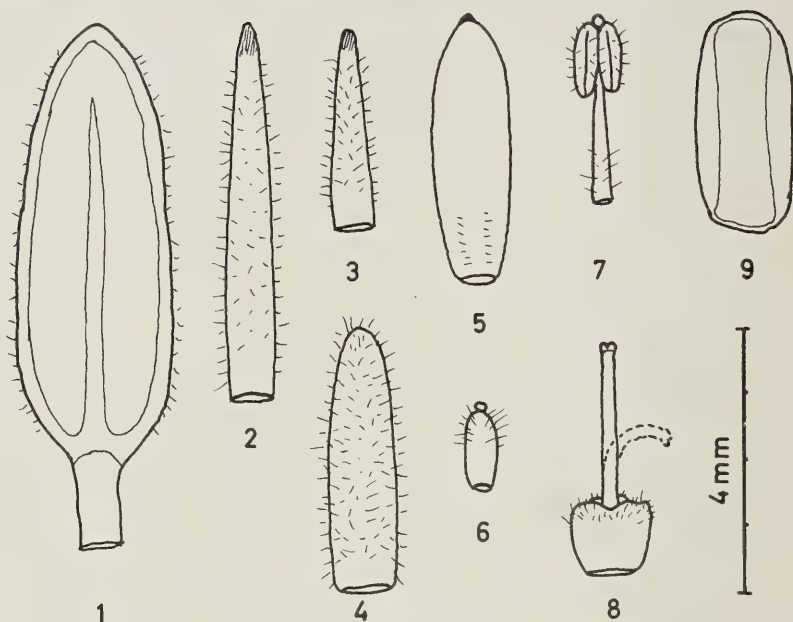


FIG. 1.

Agathosma rosmarinifolia. 1. Underside of leaf. 2. Bract. 3. Bracteole. 4. Calyx lobe. 5. Petal. 6. Staminode. 7. Anther. 8. Gynoecium. 9. Pollen.

two bracteoles at the base of the pedicel; the five staminodes, though small, are petaloid being fairly broad and pubescent with an apical gland; the style, the five filaments and the anthers are pubescent; the disc is not conspicuous and is exceeded at all times by the ovary; the ovary is tri-carpellate.

In his revision of the *Diosmeae* for the Flora Capensis, Sonder (1860) upheld Bartling's decision to place this species in *Acmadenia* but found it sufficiently different to place it in a category by itself and to state: "This, which has the habit of a *Barosma*, differs, by its capitate flowers and beardless petals, from others of this genus".

At first known only from Babilonstoringberg in the Caledon Division, this species was later found to occur on the Kleinriviersberg and on the Paardeberg, which are mountain ranges more to the south. Growing in more or less arid places amongst T.M.S. rocks at altitudes of from 500 to 1250m (1 500 to 3 800 feet), it flowers from June until November when ripening fruits may be found. Its presence in the field is betrayed by its extremely pungent odour, a most

penetrating smell, rather like garlic. In fact Lamb (1848 SAM), who collected this species in hills at Hartebeestriver, noted that it "has the odour of jackalls when fresh".

This species was apparently overlooked by Pillans (1950) in his revision of *Agathosma*.

Agathosma rosmarinifolia (Bartl.) Williams comb. nov.

Acmadenia rosmarinifolia Bartl. in *Linnaea* 17: 355 (1843).

Type: Babilonstoringsberg -[8/- Ecklon & Zeyher 813 (PRE, SAM).

Barosma foetidissima sensu Ecklon & Zeyher Enum. Plant.: 103 (1835) non *Barosma foetidissima* Bartl. & Wendl. (1824).

DESCRIPTION

Shrublets about 30 cm tall, erect, quite dense with many branches, single stemmed at base. *Branches* erect, slender, 2—3 chotomous, the bark greyish-brown, rough with leaf scars, at first clothed with a short erect pubescence later splitting and glabrescent. *Branchlets* about 5 cm long, erect, slender, yellow or purplish, densely clothed with a short erect white pubescence, densely foliate. *Leaves* crowded, spreading, *petiole* 1,5 mm long, 0,5—0,7 mm broad, pubescent, *blade* 5,5—6,5 mm long, 2—2,3 mm broad, linear-lanceolate or linear-oblong, somewhat obtuse, margins revolute, thick, gland-dotted and pubescent, upper surface dark green, glabrescent, under surface pale green nerved. *Flowers* 3—9 aggregated into terminal heads surrounded by the uppermost leaves. Each flower subtended by a *bract* 5,7 mm long, 0,7 mm broad, linear, narrowing towards the coloured apex, white below, ciliate, outer surface short-pubescent. *Bracteoles* 2, at the base of the pedicel, readily delapsing, about 3 mm long, 0,6 mm broad, pubescent, ciliate, pale in colour, apex green. *Pedicel* 1 mm long, slender, short-pubescent. *Calyx lobes* 5, about 4 mm long, 1 mm broad, linear, somewhat obtuse, greenish above, ciliate, short-pubescent, equalling the petals. *Petals* 5, 4 mm long, 1,2 mm broad, oblong-obovate, sub-obtuse, ciliolate, the apex slightly curved inwards with a callus, the nerve pubescent on the inside towards the base. *Staminodes* 5, 1,5 mm long, 0,5 mm broad, oblanceolate, ciliate, apex with a coloured gland. *Anthers* 5, before anthesis 1,1 mm long, 0,7 mm broad, oblong, clothed with short erect hairs and with a small sessile globose gland at the apex. *Filament* becoming 2,5 mm long, apex subulate, hairy below. *Pollen* obloid, 33 μ long, 15 μ diam. *Stigma* 3-fid, reddish, much the same diameter as the style when fresh. *Style* at first deflexed, eventually erect, lengthening to 2,3 mm, sparsely pubescent below. *Ovary* 3-chambered, exceeds the disc, about 0,7 diam., the apices somewhat pubescent. *Disc* not conspicuous, appears to exude nectar about the ovary.



FIG. 2.

Map showing distribution of *Agathosma Rosmarinifolia* (Bartl.) Williams.

Fruit 3-carpellate, each *carpel* 3 mm long, pubescent towards the apex, gland dotted, without horn or other process, hidden within the persistent calyx and petals. *Seed* 2,5 mm long, 1,3 mm diam., black, shining, somewhat bean-shaped.

SPECIMENS EXAMINED

CAPE—3419 (Caledon): (—AD) Babilonstoringberg, —/8/— *Ecklon & Zeyher* 813 (PRÉ, SAM), 24/2/1941 *Esterhuysen* 4967 (BOL, NBG); Hartebeesterivier, —/9/— *Lamb s.n.* (BOL, SAM); Kleinriviersberg between Stanford and Hermanus, —/9/1920 *Stokoe s.n.* (BOL 16883); Klein River Valley nr. Stanford —/9/1920 *Stokoe s.n.* (BOL 16884); Klein River Mts. near Stanford, 2000',

—/8/— without collector's name (PRE); Platberg, Hermanus, 2450', 3/6/1972 Williams 1652 (NBG), 1800', 19/11/1972 Williams 1735 (NBG). (—BC) Fairfield, 26/7/1962 Taylor 3641 (PRE, STE), 27/7/1962 Acocks 22486 (PRE).

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THE EFFECT OF SCARIFICATION, LEACHING, LIGHT, STRATIFICATION, OXYGEN AND APPLIED HORMONES ON GERMINATION OF *PROTEA COMPACTA* R.BR. AND *LEUCADENDRON DAPHNOIDES* MEISN.

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ABSTRACT

Both the seed coat and the embryo appear to contribute to the dormant condition in *P. compacta*. Germination can be improved to a greater or lesser extent by scarification, high oxygen tensions, stratification and applied hormones.

In *L. daphnoides* dormancy is mainly imposed by the seed coat which apparently acts as a barrier to oxygen diffusion to the embryo. A considerable increase in germination is brought about by scarification and high oxygen tensions applied to intact seeds. Stratification and applied hormones improve germination to a lesser extent.

Leaching and light treatments failed to improve germination in both species.

It is postulated that treatments promoting increased oxygen uptake enhance the metabolic activities of the embryos. These activities result in changes in the hormone levels in the embryo which promote radicle elongation in *P. compacta* and cotyledon expansion in *L. daphnoides*.

UITTREKSEL

DIE EFFEK VAN SAADBESKADIGING, UITLOGING, LIG, STRATIFIKASIE, SUURSTOF EN TOEGEDIENDE HORMONE OP DIE ONTKIEMING VAN *PROTEA COMPACTA* R.BR. EN *LEUCADENDRON DAPHNOIDES* MEISN. Dit wil voorkom asof beide die saadhuide en die embrio van *P. compacta* bydra tot die russtand van die saad. Ontkieming word tot 'n mindere of meerdere mate bevorder deur saadhuide beskadiging, hoë suurstof konsentrasies, stratifikasie en toegediende hormone.

In die geval van *L. daphnoides* is die russtand waarskynlik geheel en al toe te skryf aan die feit dat die saadhuide die diffusie van suurstof na die embrio belemmer. Wanneer die saadhuide beskadig word of die intakte saad aan hoë suurstof konsentrasies onderwerp word, word 'n groot toename in ontkieming te weeg gebring. Stratifikasie en toegediende hormone beïnvloed ontkieming tot 'n mindere mate.

Uitlogings- en lig behandelings het nie die ontkieming van die twee spesies bevorder nie.

Daar word voorgestel dat behandelings wat suurstof opname versnel, die metaboolse aktiwiteit van die embryos verhoog. As gevolg hiervan verander die hormoon konsentrasies in die embryos, en dit lei tot die verlenging van die kiemwortel van *P. compacta* en die vergroting van die saadlobbe van *L. daphnoides*.

INTRODUCTION

Poor germination is common within the South African Proteaceae (Vogts, 1960; Horn, 1962; Van Staden, 1966; Brown and Van Staden, 1971). This has been attributed to the presence of endogenous inhibitors (Vogts, 1960), and ineffective seed screening methods (Horn, 1962). However, germination is poor

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even with improved sorting (Van Staden, 1966; Brown and Van Staden, 1971). Although Horn (1962) did not regard inhibitors as being of importance in preventing germination, recent reports (Brown and Van Staden, 1971; Van Staden and Brown, 1972) showed that aqueous extracts of proteaceous seed contained substances that could inhibit the germination of both lettuce and water cress. Whether these inhibitors are involved in the regulation of germination, and are leached as postulated by Vogts (1960), is not known. Other than a report that light and low temperature do not increase germination (Horn, 1962), no attempt has been made to investigate the effect of any of the treatments commonly applied to overcome dormancy. The present work describes the effect of scarification, leaching, light, stratification, oxygen and applied hormones on the germination of seed of two species.

MATERIALS AND METHODS

Seed of *Protea compacta* R.Br. and *Leucadendron daphnoides* Meisn. was obtained from the South African Department of Forestry. This was hand sorted and only plump, undamaged seed used. These were germinated in petri dishes on acid washed sand (40—100 mesh) which was kept just moist with distilled water. Because temperatures above 20°C have a detrimental effect on germination (Brown and Van Staden, 1971), seed was germinated at alternating temperatures of 10°C for 16 hours followed by 20°C for 8 hours. Light (ca. 1 lm/m²) was supplied by cool white fluorescent tubes to coincide with the higher temperature period.

The protrusion of the radicle through the covering structures was used as the criterion for germination. The effect of ineffective seed sorting was further eliminated by dissecting all ungerminated seed at the end of the experimental period, and expressing the germination results as a percentage of seed that contained fully developed embryos.

RESULTS AND DISCUSSION

Mode of germination

The fruit (hereafter referred to as the "seed") in *Protea* and *Leucadendron* is an achene. The embryo is surrounded by an inner membranous testa and an outer woody pericarp of varying thickness; being thinner at the radicle end than elsewhere. In *P. compacta* the seed is elongated (ca. 15 mm long and 7 mm wide) and covered with a dense layer of fine hairs. In contrast that of *L. daphnoides* is flattened with smooth sides (ca. 9 mm long and 10 mm wide). From the side it appears to be almost circular in outline.

The mode of germination of the two species differs. In *P. compacta* the first visible sign of germination is the protrusion of the radicle through the pericarp (hereafter referred to as the "seed coat"), while in *L. daphnoides* this only occurs

after the seed coat has split. This splitting of the coat is very characteristic and always starts at the "radicle end" and extends along the edge of the flattened sides of the seed. This suggests that radicle elongation is preceded by cotyledon expansion and that without this, the radicle would not be able to emerge from within the seed coat.

Scarification treatments

When dormancy is imposed by the covering structures of the seed their complete or partial removal often results in increased germination (Barton, 1965). The coat may offer a mechanical restriction to radicle elongation or embryo enlargement (Barton, 1965; Esashi and Leopold, 1968) or alternatively it can exert its influence by acting as a barrier to the diffusion of oxygen and/or water (Barton, 1965; Edwards, 1968). The presence of hard woody coats in the species under investigation suggested that dormancy could be coat imposed.

Seed was mechanically scarified by filing away small portions of the coat. The treatments were as follows: (i) coat scarified at the "radicle end"; (ii) coat scarified at the "style end"; (iii) coat scarified midway on the side of the seed, and germinated with the scarified surface facing upwards; and (iv) the seed coat completely removed.

TABLE I

THE EFFECT OF SCARIFICATION OF THE SEED COAT ON GERMINATION OF
PROTEA COMPACTA AND *LEUCADENDRON DAPHNOIDES*
Figures are mean percentages of 8 replications of 10 seeds over 40 days.

SCARIFICATION TREATMENTS	<i>PROTEA</i> <i>COMPACTA</i>	<i>LEUCADENDRON</i> <i>DAPHNOIDES</i>
Intact seed	50 ± 5	30 ± 5
Scarified at "style end"	78 ± 5	90 ± 5
Scarified at "radicle end"	80 ± 3	75 ± 6
Scarified on side between "style" and "radicle ends"	45 ± 3	88 ± 2
Excised embryos	30 ± 8	30 ± 0

The results in Table I show that while scarification on the side of the seed had no effect on the germination of *P. compacta*, germination was significantly increased when portions of the coat at either end of the seed were removed. Such treatment could either weaken or remove the mechanical effect of the seed coat. When the coat was weakened by scarifying at the style end, "abnormal" germination, where the extending radicle pushed the cotyledons out of the covering structures, frequently occurred. Scarification on the side did not improve germination, possibly because the mechanical forces exerted by the coat were not altered sufficiently to allow the embryo to develop. These results suggest that the dormant condition of *P. compacta* is, at least in part, brought about by the mechanical restriction of the embryo by the seed coat. Where germination does

not occur, the radicle is probably unable to develop sufficiently to rupture the coat. If this were the case it might be expected that complete removal of the seed coat would result in maximal germination. However, few excised embryos germinated, as exposure to the atmosphere made them particularly subject to microbial attack. The finding that few excised embryos of *P. compacta* germinate under sterile conditions *in vitro* suggests that embryo dormancy also contributes to the dormant condition (Van Staden, Brown and Button, 1972).

In contrast with *P. compacta*, all scarification treatments resulted in significant increases in the germination of *L. daphnoides* (Table 1). In the latter species the mode of germination did not deviate from that characteristic for intact seed, irrespective of the site of scarification. Furthermore scarification in the radicle region of the seed did not enhance radicle emergence from within the coat. This indicates that the events leading to germination follow a set pattern. The first visible sign of germination being the splitting of the seed coat, apparently as a result of cotyledon expansion, followed by radicle elongation.

To obtain information about the mechanism by which the seed coat imposes dormancy on seeds of *L. daphnoides*, scarified seed was germinated in two positions. When the scarified surface was placed on the sand, only 30% germination was recorded. However, 80% germination was obtained with the scarified surface uppermost. These results suggest that exposure to the atmosphere is beneficial in increasing germination. This was tested by covering the exposed surface with lanolin, a procedure which resulted in a reduction of germination to 50%. These results suggest that the seed coat of *L. daphnoides* acts as a barrier to oxygen uptake. In addition it is significant that when the scarified surface was placed downwards on the sand, a treatment that would favour leaching of compounds from the embryo, germination was reduced to a level equal to that of the controls.

Microbial attack is probably responsible for the low levels of germination observed in excised embryos. This is suggested by the fact that embryos that germinated did so within the first twelve days of the experiment, during which time microbial activity was not very marked.

The results lead to the conclusion that dormancy of *P. compacta* is partly a result of the mechanical restriction of the coat to radicle extension and partly due to embryo dormancy. In *L. daphnoides* however, dormancy appears to be mainly coat imposed. The coat apparently exerts its influence by restricting oxygen diffusion to the embryo. Further experiments were carried out to verify these findings.

Leaching treatments

Coat imposed dormancy may be due to the presence of inhibitors in the coat (Bradbeer, 1968; Irving, 1968) or alternatively their outward diffusion from the

embryo may be impeded (Webb and Wareing, 1972). Although Vogts (1960) has postulated that inhibitors are involved in the regulation of germination of proteaceous seed, and such compounds have been extracted from the seed (Van Staden and Brown, 1972), their actual involvement in imposing dormancy has not been shown.

The effect of leaching on germination was investigated by the following procedures: Seed was shaken in 100 ml distilled water for 4, 8 and 12 days respectively. During this time the water was renewed every 2 days. The bulked leachates were concentrated to 100 ml, their pH adjusted to 2.0 upon which they were extracted and assayed for inhibitors as previously described (Van Staden

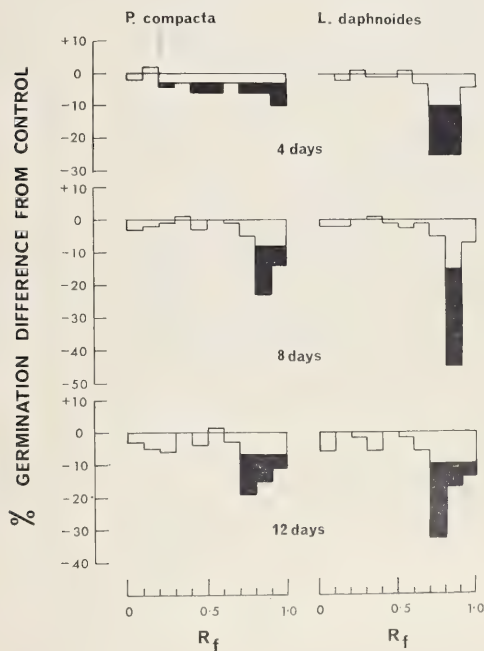


FIG. 1.

THE EFFECT OF SEED LEACHATES OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* ON GERMINATION OF GRAND RAPIDS LETTUCE SEED IN LIGHT.

Fifteen grams seed leached. Shaded areas represent differences significant at the 1% level.

and Brown, 1972). In Figure 1 it can be seen that inhibiting substances were removed from the intact seed by leaching. The inhibition produced by leachates increased up to 8 days, whereafter it remained more or less constant. Most of the inhibiting activity was found between $R_{10.8}$ and 1.0, which corresponded with that previously reported for embryos and seed coats (Van Staden and Brown, 1972). In spite of the evidence indicating removal of inhibitors by leaching, the treatment did not increase germination (Table 2). Although this suggests that the inhibitors may not be active in regulating germination the

TABLE 2

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF LEACHING SEEDS BY SOAKING IN DISTILLED WATER.

Figures are mean percentages of 8 replications of 25 seeds over 63 days.

TIME (DAYS)	<i>PROTEA COMPACTA</i>	<i>LEUCADENDRON DAPHNOIDES</i>
0	49 $\pm$ 11	27 $\pm$ 1
4	6 $\pm$ 1	11 $\pm$ 1
8	2 $\pm$ 1	4 $\pm$ 1
12	0	7 $\pm$ 1

low germinability may be the result of other factors related to the treatment, such as oxygen stress.

To eliminate inadequate aeration seed was leached intermittently (12 hours each day) in running water for 4, 8 and 12 days respectively. Care was taken that they never dried out. Under these conditions it was considered that seeds would receive sufficient aeration for germination. However, subsequent germination showed the same pattern as seed that was submerged in water (Table 3).

TABLE 3

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INTERMITTENT LEACHING OF SEED IN RUNNING WATER.

Figures are mean percentages of 8 replications of 25 seeds over 63 days.

TIME (DAYS)	<i>PROTEA COMPACTA</i>	<i>LEUCADENDRON DAPHNOIDES</i>
0	45 $\pm$ 8	26 $\pm$ 4
4	20 $\pm$ 4	9 $\pm$ 2
8	17 $\pm$ 4	6 $\pm$ 1
12	9 $\pm$ 2	9 $\pm$ 2

If the dormant state of the seed is the result of high inhibitor concentrations in the embryos that cannot be leached through the seed coat, then scarification and placement of the seed in a position to favour leaching would be expected

to increase germination. Such a treatment applied to *L. daphnoides* gave germination no different to intact controls. According to the evidence obtained it would appear as if the seed coats do not exert an influence on germination by impeding the leaching of inhibitors. If inhibitors play a rôle in the control of germination it is apparently not an over-riding effect.

The fact that the germination of both species is progressively inhibited with increasingly high levels of hydration (Tables 2 and 3) is probably due to the phenomenon of "water-sensitivity". Here a state of dormancy is induced by an over-abundant supply of moisture (Hay, 1962). According to Hay (1962) and Negbi, Rushkin and Koller (1966) this inhibition of germination is due to the resistance of the water layers to diffusion of oxygen into the embryo.

Stratification treatments

Van Staden *et al.* (1972) have shown that in *P. compacta* germination is only partly regulated by the seed coat because a large proportion of excised embryos do not germinate when placed under favourable conditions for germination. In *L. daphnoides* dormancy appears to be wholly coat imposed. It is well known that embryo and coat imposed dormancy may be overcome by a period of storage under moist conditions at low temperature (Wareing and Saunders, 1971).

TABLE 4

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INCUBATION OF SEED UNDER MOIST CONDITIONS AT 5°C AND 25°C

Figures are percentages of 250 seeds.

TEMPERATURE	TIME (DAYS)	<i>PROTEA COMPACTA</i>	<i>LEUCADENDRON DAPHNOIDES</i>
	0	46	20
5°C	30	59	30
	60	59	23
	90	65	18
25°C	30	3	5
	60	0	3
	90	0	0

The effect of stratification on the germination of both species was investigated by imbibing seed on moist filter paper for 24 hours and then incubating them at 5° and 25°C for 0, 30, 60 and 90 days respectively. After incubation the seed was germinated under standard conditions.

The results presented in Table 4 show that incubation of seed at 25°C decreased germination significantly. Stratification of seed of both species at 5°C for 30 days increased germination. However, longer periods of stratification did not increase germination further. The effect of stratification is apparently to increase the ability of cotyledons to split the coat in *L. daphnoides* and the radicle to pierce the coat in *P. compacta*.

Light treatments

Experiments with red and far-red light treatments supported the contention (Horn, 1962) that light does not influence the germination of proteaceous seed.

Oxygen treatments

The effect of the seed coat on free exchange of oxygen was investigated by germinating seeds of *P. compacta* and *L. daphnoides* in air, oxygen and nitrogen. The seed was placed on moist sand in 500 ml flasks. The flasks were evacuated and then flushed with the appropriate gas. At 4-day intervals the gas was renewed and germinated seed removed. Care was taken to ensure that atmospheric pressure was not exceeded in the flasks.

TABLE 5

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF INCUBATING SEED IN AIR, PURE OXYGEN AND PURE NITROGEN.

Figures are mean percentages of 4 replications of 20 seeds.

TREATMENT	<i>PROTEA COMPACTA</i>	<i>LEUCADENDRON DAPHNOIDES</i>
AIR	47 ± 17	12 ± 7
PURE OXYGEN	72 ± 7	85 ± 14
PURE NITROGEN	0	0

Oxygen increased germination (Table 5), the effect being more marked in *L. daphnoides* than *P. compacta*. No germination was recorded in the absence of oxygen and when after 44 days the nitrogen was replaced by oxygen *L. daphnoides* gave a 55% germination response, indicating that seed had not suffered adversely in the absence of oxygen. *P. compacta* seed, however, failed to germinate. These results clearly suggest that in both species the seed coat may act as a barrier to gaseous diffusion and hence impose dormancy. Furthermore it seems most likely that the deleterious effect of prolonged soaking (Tables 2 and 3) is due to the resistance of the water layers to the diffusion of oxygen. The difference in response to oxygen, after nitrogen treatment, may be related to fundamental differences in the metabolism of *P. compacta* and *L. daphnoides* seed.

Applied hormones

Growth promoters such as kinetin and gibberellic acid can substitute for the chilling requirement of certain seeds (Webb and Dumbroff, 1969; Baskin and Baskin, 1970). In order to determine whether they can bring about a similar effect in the seed of *P. compacta* and *L. daphnoides*, seed was soaked for 24 hours in each of a range of solutions of benzyladenine (BA) and kinetin (1, 10, 50 mg/l), and gibberellic acid (1, 10, 100 mg/l).

TABLE 6

THE EFFECT ON GERMINATION OF *PROTEA COMPACTA* AND *LEUCADENDRON DAPHNOIDES* OF SOAKING SEED IN KINETIN, BENZYLADENINE AND GIBBERELLIC ACID.

Figures are mean percentages of 4 replications of 10 seeds after 72 days.

CHEMICAL	CONCENTRATION	<i>PROTEA COMPACTA</i>	<i>LEUCADENDRON DAPHNOIDES</i>
	Control	57 ± 3	20 ± 2
Kinetin	1 mg/l	67 ± 5	13 ± 1
	10 mg/l	78 ± 1	33 ± 4
	50 mg/l	58 ± 3	30 ± 2
Benzyladenine	1 mg/l	72 ± 3	35 ± 3
	10 mg/l	54 ± 5	20 ± 2
	50 mg/l	76 ± 2	10 ± 1
Gibberellic Acid	1 mg/l	62 ± 3	23 ± 2
	10 mg/l	68 ± 1	30 ± 2
	100 mg/l	66 ± 1	23 ± 3

Although germination in both species can be increased by treatment with the three growth promoters, the species differ in their responses (Table 6). Kinetin (10 mg/l), BA (50 mg/l) and GA₃ (10 mg/l) elicit highest germination in *P. compacta*, whereas in *L. daphnoides* kinetin (10 mg/l), BA (1 mg/l) and GA₃ (10 mg/l) are equally effective. These results agree with those obtained with excised embryos under sterile conditions (Van Staden *et al.*, 1972).

The effect of applied hormones may be to increase radicle extension in *P. compacta*, as has been shown to occur in lettuce by Haber and Luipold (1960) and in *Acer pseudoplatanus* by Pinfield and Stobart (1972). In *L. daphnoides* the effect may be to promote cotyledon expansion as found by Ikuma and Thimann (1963) in lettuce; Kursanov, Kulaeva and Mikulovich (1969) in pumpkin and Esashi and Leopold (1969) in *Xanthium*.

CONCLUSIONS

The germination responses of seed to a wide range of treatments show that both the coats and embryos could contribute to the dormant condition in *P. compacta* and *L. daphnoides*.

Although inhibitors are leached from intact seed, no evidence could be found that they are actually involved in the regulation of germination, or that their leaching is a prerequisite for germination. In addition the covering structures do not appear to restrict the leaching of such compounds from the embryo.

In *P. compacta* the seed coat appears to mechanically restrict radicle elongation, and to a lesser extent, to retard oxygen uptake. These effects are overcome to a greater or lesser degree by scarification, high oxygen tensions and stratification. The effect of stratification may be due to physical changes in the covering structures, enabling the radicle to emerge more readily, or to chemical changes in the embryo enabling the radicle to develop sufficient thrust to pierce the coat.

In *L. daphnoides* the seed coat imposes dormancy by acting as a barrier to oxygen diffusion to the embryo. Scarification treatments which broke that barrier, as well as high oxygen tensions applied to intact seed resulted in dramatic increases in germination. The poor germination obtained after prolonged soaking and leaching may be due to an increased barrier to oxygen brought about by the over-abundance of water. Stratification increases germination, an effect which can perhaps be attributed to the indirect influence of low temperature on oxygen diffusion to the embryo. Wareing (1969) has stressed that for stratification to be successful seeds must be fully imbibed and have adequate aeration. It is postulated that chilling treatments lead to physical changes in the covering structures which then allow greater penetration of oxygen. This in turn leads to increased metabolic activity, resulting in changes in hormone levels that can promote radicle elongation in *P. compacta* and cotyledon expansion in *L. daphnoides*. Both these growth phenomena have previously been shown to be affected by hormones (Ikuma and Thimann, 1963; Pinfield and Stobart, 1972), while in the present study gibberellins and cytokinins have been shown to increase germination. It is possible that the effect of oxygen in increasing germination is mediated by changes in endogenous hormone levels. This possibility is at present under study.

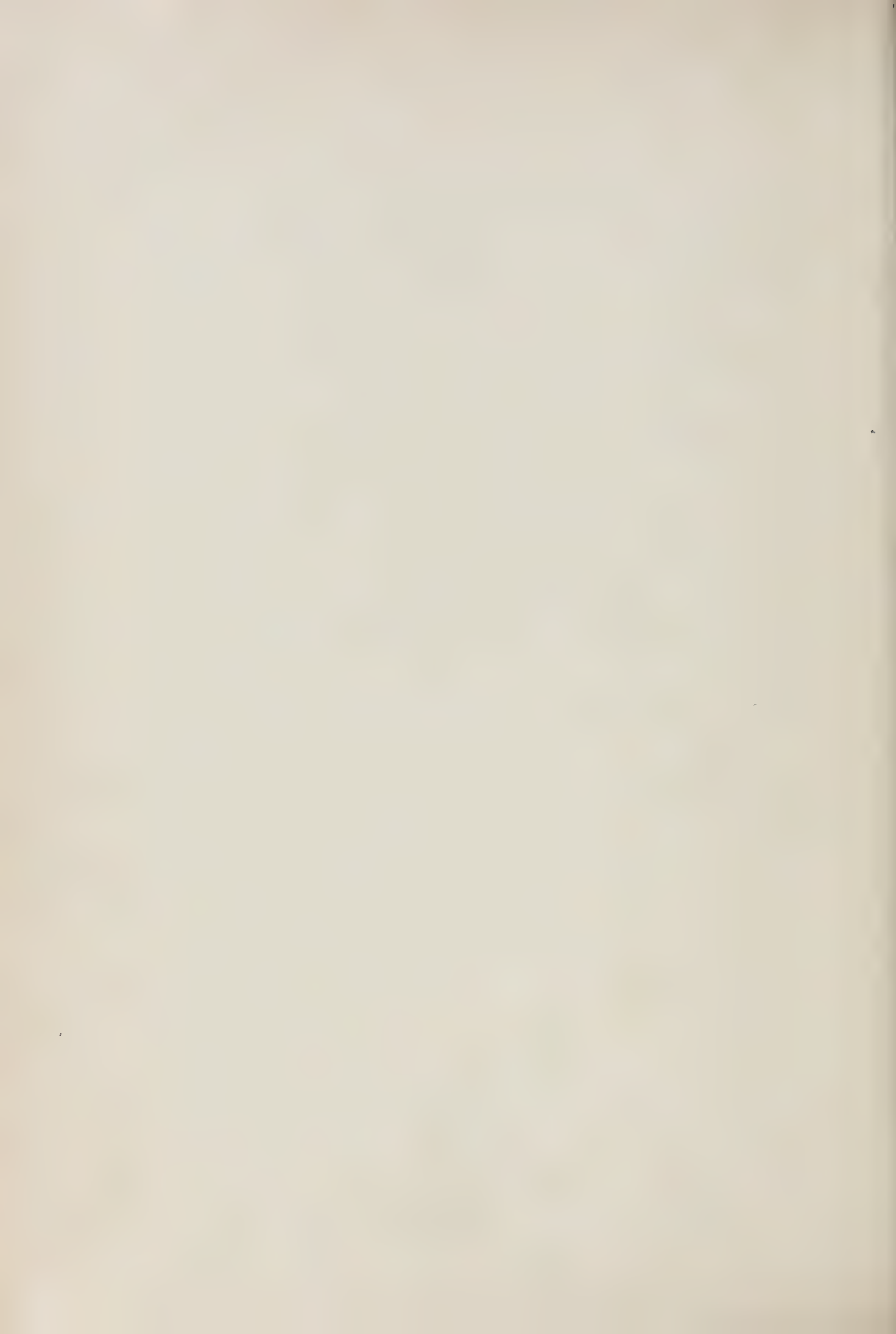
ACKNOWLEDGEMENTS

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BOOK REVIEWS

CHEMISTRY OF FUNGICIDAL ACTION by R. J. Lukens, edited by A. Kleinzeller, Philadelphia; G. F. Springer, Evanston; H. G. Wittmann, Berlin, with pp. 136, 8 figures. London: Chapman and Hall Ltd.; Berlin, Heidelberg and New York; Springer-Verlag, 1971. £5.00.

The material is well presented and well edited in a book with hard cover (linen) of 25 × 17 cm format.

This is a monograph with data "based on literature of plant pathology, pharmacology and industrial preservatives." The first chapter includes a brief historical introduction together with notes on the importance and general actions of fungicides. Chapters two to four briefly summarise the measurement of fungitoxicity, methods of application, dispersal, deposition, retention, persistence, formulation and cell penetration. The main topic, chemistry of fungicidal action, is introduced in chapter five, in which sites of action are discussed.

Fungicides which interfere with the metabolism of the cell are of two types. The most important are those reacting with cellular constituents. These are discussed in chapter six, while the second type, those affecting enzyme systems, are dealt with in chapter seven. Chapter eight deals with structure-activity relationships of certain fungicides, while the final chapter discusses the action of the fungus on the fungicide.

An appendix gives the structure and uses of a number of the better-known fungicides. There is also an extensive subject index, and a comprehensive list of references. These references, together with the manner of presentation of the subject matter, makes this an extremely suitable reference work for senior and postgraduate students. Agricultural extension workers will also find it useful. It is, however, unsuitable for laymen or for the research chemist.

The subject matter is of a universality which makes it equally suitable for South African and overseas conditions.

The author has ably covered an extremely wide field but there are no half-tone illustrations and few equations, graphs or tables. The impression gained is that the author's space was restricted by the publisher.

P. S. VAN WYK.

INDEX TO SOUTH AFRICAN PERIODICALS.

We wish to draw to your attention the annual *Index to South African Periodicals*, in which this journal is indexed. This is an alphabetical list of articles appearing in South African periodicals and is arranged under the name of the author and the subject of the article. It should be of great value to all research workers concerned with current South African material.

The *Index* may be consulted in the Reference Department of the Johannesburg Public Library and in most of the larger libraries in the country. The current issues are also obtainable from the Johannesburg Public Library at R10.00 per annual volume.

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Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION, CONCLUSION, ACKNOWLEDGMENTS, etc.

Tables and illustrations should be on separate sheets. **Figures and graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm × 12 cm (7" × 4½"). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

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Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations** and **herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

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Chrysophyllum magalismontanum Sond. in Linnaea 23: 72 (1850). Type: Magaliesberg, Zeyher, 1849 (S, holo.; BOL!, SAM!).

Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

Pouteria magalismontana (Sond.) A. Meeuse in Bothalia 7: 335 (1960).

Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. 3: 641 (1898). Syntypes: Angola, Welwitsch 4827, 4828, 4829 (BM!).

Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal Wilms 1812 (B†, holo.; K!).

Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. 105: 37 (1958).

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These should be given in the text as follows: Jones (1968) or (Jones, 1968) or, where reference to a specific page is required, Jones (1968:57) or (Jones, 1968:57). **Literature cited** should be arranged alphabetically by surnames, chronologically within each name, with suffixes a, b, etc., to the year for more than one paper by the same author in that year. Titles of **periodicals** must be abbreviated according to the *World List of Scientific Periodicals*, 4th ed., London: Butterworth or when unable to trace the title in this list (as will be the case in taxonomic papers where abbreviations of 18th and 19th century periodicals are required) the abbreviations given in *Botanico-Periodicum-Huntianum*, Pittsburgh: Hune Botanical Library, 1968, should be followed. Periodical titles should be underlined once (for italics). If an author is unable to determine the correct abbreviation of a journal title he is advised to type it out in full and leave its abbreviation to the Editor. Titles of **books** should be underlined and given in full, together with the place of publication, name of the publisher and an indication of the edition if other than the first; e.g.:

Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy*. Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia*. *Jl S. Afr. Bot.* 26: 139-148.

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OXALIS DINES*, A NEW SPECIES FROM THE WESTERN CAPE

ROBERT ORNDUFF

(Department of Botany, University of California, Berkeley)

ABSTRACT

On morphological, geographical, and cytological grounds, *Oxalis disticha* Jacq. var. *alba* Salter is raised to specific status as *O. dines* Ornduff.

ERRATA

Vol. 39 (2): 141-178. A reappraisal of type and authentic specimens of Basidiomycetes in the Van der Byl Herbarium, Stellenbosch, by Derek A. Reid.

Figs. 1-40 were incorrectly reduced. The corrected magnifications are as follows:-

Figs. 1-12 $\times 650$

Figs. 13-22 $\times 700$

Figs. 23-32 $\times 670$ (excepting 25a, 26a, 27a, $\times 1120$)

Figs. 33-36 $\times 770$ (excepting 35 and 36, $\times \frac{1}{2}$)

Figs. 37-40 $\times \frac{2}{3}$

approximately 50-80 mi N of Cape Town. This series of three disjunct populations occupies an area that is approximately 30 miles in length. *Oxalis dines*

Accepted for publication 5th February, 1973.

* Studies supported in part by grants from the National Science Foundation, the Bache Fund of the National Academy of Sciences (both USA), and the CSIR. I am indebted to a number of colleagues and friends in South Africa who assisted my studies in numerous ways, and to Patricia Watters for technical assistance.

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UITTREKSEL

OXALIS DINES, 'N NUWE SOORT VANAF DIE WES-KAAP.

Vir morfologiese, geografiese en sitologiese redes word *Oxalis disticha* Jacq. var. *alba* tot soortrang verhef as *Oxalis dines* Ornduff.

During field work associated with studies of reproductive systems of various heterostylous *Oxalis* species in the Cape Province I collected all five species of section Campanulatae, including the two varieties of *O. disticha* Jacq. that were recognized by Salter (1944). Subsequent studies of these two varieties indicate that they are distinct from each other in a number of characteristics beyond those mentioned by Salter and lead to the conclusion that each merits specific status. As a result, I am raising *O. disticha* var. *alba* Salter to specific rank:

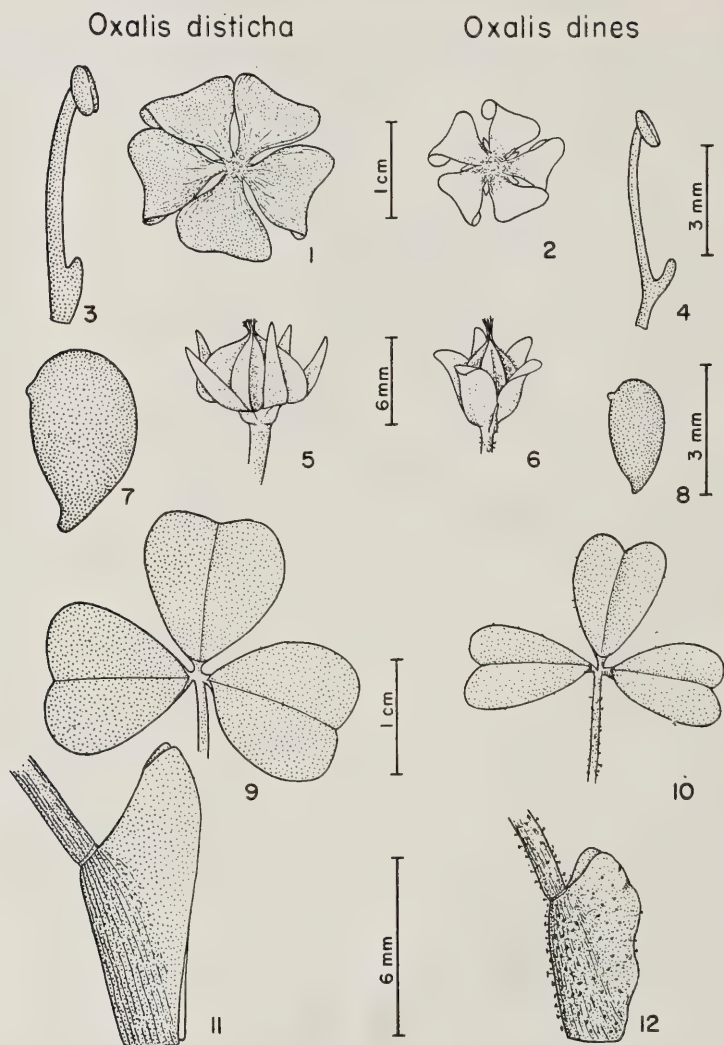
Oxalis dines Ornduff, stat. et nom. nov.

O. disticha Jacq. var. β *alba* Salter in Jl S. Afr. Bot. Suppl. Vol. 1: 187.
Holotype *Schlechter* 10874, BOL!

Oxalis dines differs from *O. disticha* in a number of morphological characteristics (Figure 1; Table 1). In addition, *O. dines* has $n = 7$ (based on Ornduff 7471, N end of Botterkloof Pass, UC) and *O. disticha* has $n = 8$ (based on Ornduff 7166, 1 mi N Pools siding; Ornduff 7297, nr Koperfontein, both UC). The floral scent of *O. dines* is intense and distinctively different from the weaker scent of *O. disticha*. The two species are allopatric: *O. disticha* is known only from seasonal pools in the vicinity of Pools (siding) NE of Piketberg, from the vicinity of Piketberg, and from the vicinity of Koperfontein, localities that are approximately 50–80 mi N of Cape Town. This series of three disjunct populations occupies an area that is approximately 30 miles in length. *Oxalis dines*

Accepted for publication 5th February, 1973.

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FIGS. 1—12.

Morphological characters of *Oxalis disticha* and *O. dines* of taxonomic value. Fig. 1, 2, corollas; stippling indicates areas of yellow pigmentation. Fig. 3, 4, stamens. Fig. 5, 6, capsules. Fig. 7, 8, seeds after removal of testa. Fig. 9, 10, leaves. Fig. 11, 12, stipules and base of petioles.

likewise is restricted in distribution, known only from a few localities NE of Clanwilliam and from the vicinity of Clanwilliam. Both species are aquatic and occupy seasonal pools; Salter (1944: 187) erred in stating that *O. dines* "does not occur in clay" since the single population of this species that I observed occupied the heavy clay soil in the bed of a drying pool. I have not been able to locate populations of either species beyond some of those cited by Salter (1944: 186–187) and I believe that others of the populations cited by him are now extinct. In my opinion, *O. disticha* may be as closely related to *O. uliginosa* Schlechter (also $n = 8$, based on *Ornduff* 7209, ca 19 mi NE Kamieskroon), as it is to *O. dines*.

Artificial hybrids between *Oxalis disticha* and *O. dines* are obtained only with great difficulty; the single hybrid plant that I have grown to maturity (*O. dines* 7471 $\times$ *O. disticha* 7297) produced pollen with a stainability of 58% in aniline blue-lactophenol. However, this figure is undoubtedly an overestimate of the pollen fertility of the interspecific hybrid since a number of grains scored as viable were misshapen and probably non-functional.

The species is named in honour of Mrs. Enid du Plessis; the specific name is the genitive singular of the Latinized Greek word *dine*, an anagram of Enid, but it also means "of a whirlwind".

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SALTER, T. M., 1944. The genus *Oxalis* in South Africa. *Jl S. Afr. Bot. Suppl.* Vol. 1: 1–355.

TABLE 1.

Characters distinguishing *Oxalis dines* from *O. disticha*. See also Figs. 1–12.

	<i>O. dines</i>	<i>O. disticha</i>
Flower colour	predominantly white	yellow
Corolla length	1,3–1,5 cm	1,8–2,2 cm
Filament tooth	prominent, cylindric	short, deltoid
Sepal length	4–6 mm	5–8 mm
Sepal shape	ovate	narrowly ovate-triangular
Leaflet shape	narrowly obcordate	broadly obcordate
Pubescence	copious, esp. on petiole	sparse or absent
Stipule	sinus divided to petiole	fused below sinus
Floral scent	strong, distinctive	weak, distinctive
Haploid chromosome no.	7	8

NEW TAXA IN THE GENUS *ERICA*

H. A. BAKER

ABSTRACT

Five new species and one new variety of *Erica* are described.

UITTREKSEL

NUWE TAXSA IN DIE GESLAG *ERICA*.

Vyf nuwe *Erica* soorte en een nuwe variëteit word beskryf.

INTRODUCTION

Material of several species of *Erica* was submitted to the author for determination during the past year. This included five apparently undescribed species which are now enumerated here.

Erica obconica H. A. Baker, sp. nov. (Ericaceae—Ericoideae) Melastemon.

Frutex erectus, validus, circa 1 m altus. *Rami* numerosi, tomentosi pilis variabilis aliquot longioribus et compositis. *Folia* 3-nata, 6-9 mm longa cum petiolis ciliatis, effusa vel squarrosa, primo imbricata, lanceolata vel late lanceolata, plus minusve plana, dilute sulcata, glabra, ad marginem scariosa, mucronata. *Flores* terminales, umbellati, circa 6-nati, corollini; pedunculi 1,2 cm longi, ut in ramis tomentosi; bracteae, 2 subapproximatae, 2,5 mm longae, lineares, acutae, aliter velut in sepalis, 1 remota, circa 3 mm longa, variabilis, interdum linearis, interdum spathulata parte supera foliacea. *Sepala* circa 3 mm longa, anguste ovata, concava, imbricata, carinata et ad apices sulcata, scariosa, glabra, margine sparsum dentatum et setis caducis, mucronata, rosea pillida. *Corolla* 5 mm longa, late obconica, sicca, glabra, varie rosea; lobi continui, 2,5 mm longi, rotundati, subobtus. *Filamenta* late linearia aliquantum decessens; antherae inclusae sed manifestae, 2 mm longae, laterales, anguste ellipticae, muticae, scaberulae, super porum parce productae, castaneae; poro fere pars 3/8 lobi. *Ovarium* ovoideum, glabrum; stylo exserto; stigmatibus cyathiformi.

Erect sturdy shrub to 1 m or so. *Branches* tomentose with mixed hairs some of which are compound and longer than the average, numerous. *Leaves* 3-nate, 6-9 mm long inclusive of the ciliate petiole, erect-spreading to squarrose, imbricate at first, variable in shape from narrow lanceolate to broad lanceolate, more or less flat, faintly sulcate, glabrous, scariosus-edged and mucronate. *Flowers* terminal in umbels of about 6, corolline; peduncles 1,2 cm long,

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tomentose as the branches; bracts, 2 subapproximate, 2.5 mm long, linear, acute, otherwise like the sepals, 1 remote, about 3 mm long, variable in shape, sometimes similar to the upper two, sometimes spatulate and foliaceous in the upper part. *Sepals* about 3 mm long, narrowly ovate, concave, imbricate, keeled and sulcate towards the apex, scarious, glabrous, on the margins sparsely toothed with caducous setae, pale pink. *Corolla* 5 mm long, wide obconic, dry, glabrous rose-pink of various shades; lobes continuous, $2\frac{1}{2}$ mm long, rounded and subobtuse. *Filaments* broad-linear tapering slightly to the apex; anthers included but manifest, 2 mm long, lateral, narrow-elliptic, scarcely produced above the pore, scaberulous, muticous, bright chestnut-brown as in the ovary; pore about $\frac{3}{8}$ of the cell in length. *Ovary* ovoid, glabrous; style exserted; stigma cyathiform.

Type: CAPE—3321 (Ladismith); Langeberg, West of Garcia's Pass; Mozambique Kop (-CC) on steep Southerly slopes and cliffs, alt. 1280 m. 29/10/1967 *Esterhuysen* 31780 (Holotype, BOL).

This species is placed in the Section *Melastemon* with some reserve as the anthers are not produced above the pores to any extent. Nevertheless they are very scabrid at the top and often incurved, giving the appearance of having such a production. Moreover, the species does not fit into any other Section. It may be said to be related to *E. cubica* L. which is also found in this neighbourhood inter alia. It differs, however, from the latter in many important respects. Even allowing for the fact that *E. cubica* is very variable and common, even up to Natal, *E. obconica* cannot be regarded as a variant thereof and is, in the author's opinion, worth specific rank.

Erica granulatifolia H. A. Baker, sp. nov. (Ericaceae-Ericoideae) *Melastemon*.

Fruticulus erectus, robustus ad circa 30 cm altus. *Rami* ascendens, tomentosi, pilis longitudinibus variantes. *Folia* 3—nata, circa 4 mm longa, lanceolata vel ovalis, dorsis late vel anguste apertis, late effusa vel squarrosa subterficialis granulatis, scabridisetosa setis caducis. *Flores* in ramulis terminales brevis, solitarii vel binati sed ad apices ramorum umbellati, floribus multis et aliquot axillares apparentur; pedunculi 2.5 mm longi, ut in ramis tomentosi; bracteae remotae, circa 1 mm longae, linearilanceolatae, ciliatae. *Sepala* 1—1.25 mm longa, late nervata, marginibus scariosis, apicibus sulcatocarinatis, concava, alba sed nervis discoloribus, glabra, setociliata setis caducis. *Corolla* 2.5—3 mm longa, obconica, sicca, glabra, roseola; lobi continui, 1.5 mm longi subacuti. *Filamenta* linearia, lata, aliquantum decessens; antherae inclusae sed manifestae, circa 1 mm longae, laterales, oblongae, infra obtusae sed ad apicem decessens et super porum acutescens scabridae, muticae; poro fere pars dimidio lobi. *Ovarium* globosum, sulcatum, ad apicem villosum; stylo exserto, saepe curvo; stigmatibus cyathiformi.

Erect robust shrublet to 30 cm or so. *Branches* tomentose with hairs of varying length. *Leaves* 3-nate, about 4 mm long, lanceolate to ovate, narrowly to widely open-backed, spreading to squarrose, the under surface granulate, the margins scabrid-setose, the setae caducous. *Flowers* terminal on very short branchlets, solitary or binate but umbellate at the branch ends with many flowers, some apparently axillary, corolline; peduncles 2,5 mm long, tomentose as branches; bracts remote about 1 mm long, linear-lanceolate, ciliate. *Sepals* 1–1,5 mm long, ovate, broadly nerved and with scarious margins, sulcate-keel-tipped, concave, glabrous, setose-ciliate, the setae caducous, white except for the discoloured nerves. *Corolla* 2,5–3 mm long, obconical, dry, glabrous, pale rose; lobes continuous, 1,5 mm long, subacute. *Filaments* linear, broadish below, tapering upwards; anthers manifest, about 1 mm long, oblong, obtuse below but narrowed at the apex into a rough scabrid point produced above the cells in varying degrees and often those of the two cells diverging, mucous; pore half as long as the cell. *Ovary* globose, villous on the apex; style exserted, often curved; stigma cyathiform.

Type: CAPE—3321 (Ladismith): Mozambique Kop (-CC) on steep Southerly slopes at c. 1219 m 29/10/1967 *Esterhuysen* 31779 (Holotype, BOL).

This taxon is fairly placed in the section *Melastemon* since it has, in varying degrees, most of the characters as described for that section. It comes nearest to *E. nervata* Guthrie & Bolus in the key for the section in Fl. Cap. 4:45 (1909), especially in having open-backed leaves and glabrous sepals but there are many other important differences that distinguish the two and, in the author's opinion, merit *E. granulatifolia* the rank of species.

Erica pustulata H. A. Baker, sp. nov. (Ericaceae-Ericoideae) Pleurocallis.

Frutex erectus, validus, circa 0,6 m altus. *Rami* ascendens, glabri. *Folia* verticillata, 4–5 mm longa, incurvata, imbricata, linearia, sulcata, glabra. *Flores* pseudoaxillares, ramulis minimis abortivis, solitarii, versus apices ramorum fasciculati; pedunculi c. 5 mm longi, ad bases minute pubescentes; bractae 3, 4–5 mm longae, subapproximatae ad remotae, foliaceae. *Sepala* 4–5 mm longa, linearia sed ad basi anguste, brevi ovata, foliacea et similis pedunculis bracteisque viscida. *Corolla* 7 mm longa, ovoïdo-urceolata, ad fauce non contracta, 8-nervis, nervis quattuor prominens, pseudotetragona, prominens pustulata, glabra, viscidissima, lutea; lobis continuis, 1 mm longis, obtusis. *Filamenta* ligulata; antherae inclusae, 1,25 mm longae, basi dorsifixae, late cuneatae, bipartitae, laevigatae, muticae, atrobrunneae. *Ovarium* late turbinatum vel late oblongum, dense albavillosum; stylo exserto, stigmatibus capitate.

Erect sturdy shrub to about 0,6 m high. *Branches* ascending, glabrous. *Leaves* 4–5 mm long, spirally whorled, erect-spreading, incurved, imbricate, linear, sulcate, glabrous. *Flowers* pseudo-axillary with very small aborted branchlets, solitary in short clusters at the ends of the branches; peduncles c.5

mm long, minutely pubescent at the lower ends, viscid; bracts 3, subapproximate to remote, 4–5 mm long, foliaceous. *Sepals* 4–5 mm long, linear with a short, narrow, ovate base, foliaceous and, like the peduncles and bracts, viscid, probably from the corolla. *Corolla* 7 mm long, ovoidurceolate, not contracted at the throat, 8-nerved of which 4 are very prominent, making the corolla appear tetraginous, the whole especially along the raised nerves, with prominent pustulate glands, glabrous, extremely viscid, yellow; lobes continuous, about 1 mm long, obtuse. *Filaments* ligulate; anthers included, 1.25 mm long, basically dorsifixed, broad cuneate, bipartite, smooth, muticous, dark brown; pore c. 1 mm long. *Ovary* broad turbinate to broad oblong, densely white-villous; style exserted; stigma capitate.

Type: CAPE—3419 (Caledon) above the dams on Mossel River at Hermanus (-AC), at about 609 m, 11/10/1971 *I. Williams 1552* (Holotype, BOL).

This species is of great beauty, the flower being of a clear, bright yellow. Although, in the type locality, it is associated with *E. longifolia* Ait. and *E. onosmaeflora* Salisb. and bears some likeness to them, it is not, after careful study, considered to be a variety of either or a hybrid. Most parts of the plant are smaller to a considerable degree than those of the *longifoliae* of the Section Pleurocallis and of the other sections of Syringodea and it must be considered to be an exception therein. There is no other place for it in the genus. Apart from the dimensions and the shape of the corolla, another feature, rare in the genus, is the pustulate corolla which, in this species, is extremely outstanding. Another plant that has this feature in a very modified manner is a variety of *E. longifolia*, var. *viridis*, collected by the author in the Elgin neighbourhood, but, in all other respects except colour, it is like the type variety.

This species has not, apparently been collected hitherto and may be, like so many species in this genus, local. It is, however, abundant in the type locality.

***Erica uysii* H. A. Baker, sp. nov. (Ericaceae-Ericoideae) Eurystoma.**

Frutex erectus, validus ad 2 m altus. *Rami* ascendens, ramulis multis, brevibus, tomentosi pilis inequalibus, aliquot ramosis, demum glabri. *Folia* 3—nata, c. 1 mm longa erecto-effusa arte imbricata squarrescens, oblonga vel elliptica, obtusa, sulcata, crenata, crassa, nitida, glabra, seticiliata, pilis aliquot ramosis. *Flores* pro parte maxima 3—nata, interdum 4—nata, terminales sed, interdum, pseudo-laterales, cernui; pedunculi 3,50 mm longi, indumentum ut in ramis; bractae, 2 subapproximatae, 1 remotae, sepaloideae sed angustatae. *Sepala* c. 2,50 mm longa ad corollae premens, ovata, concava, apicibus sulcatis, scariosa, glabra, breviter et dense seticiliata. *Corolla* 3–3,5 mm longa, depressogloboso-urceolata, ad fauci angustatae, ad basi quadrifidae, aspectu tetragona, glabra, rosea; lobis minus quam 1 mm longis, leviter effusis, obtusis. *Filamenta* linearia sursum decessens et flexa; antherae minus quam 1 mm longae, mani-

festae vel exsertae, oblongae, obtusae bipartitae, scabrae, junctae basi ponticulo parvulo ex connectivo, terminalis, plus aristae subulatae, dentatae, libri, plus minusve quam longae quam cellulae. *Ovarium* turbinatum, dense hispidum; styleo exserto; stigmate simplici.

A sturdy, erect shrub to about 2 m high. *Branches* ascending with numerous small branchlets, some abortive, tomentose, with hairs of unequal length, some of which are branched, becoming glabrous after the cortex has split and fallen off. *Leaves* 3—nate, about 1 mm long, erect-spreading and closely imbricate at first becoming squarrose, oblong or elliptic, obtuse, sulcate, crenate, thick and shining, glabrous, setose-ciliate with some hairs branched. *Flowers* mostly 3—nate but occasionally 4—nate, terminal but sometimes appearing axillary from the abortion of the branchlets, cernuous, corolline; flowers rather bunched towards the end of the branches; peduncles 3, 5 mm long, indumentum as in branches, curved; bracts, 2 approximate, 1 remote like the sepals but smaller. *Sepals* 2, 5 mm long, pressed to the swollen corolla tube, ovate, concave, keel-tipped, scarious, glabrous, shortly and densely setose-ciliate. *Corolla* 3—3,5 mm long, depressed-globose-urceolate, narrowed at the throat, 4-cleft giving a tetragonous appearance, dry, glabrous, rose-coloured but white under the sepals; lobes less than 1 mm long, slightly recurved, obtuse. *Filaments*, linear, narrowing above and flexuous; anthers manifest to exserted, less than 1 mm long, oblong, obtuse, bipartite, scabridulous, narrowed below and joined together by a minute bridge of anther connective, to which the filament is attached, appendiculate; awns subulate, profusely dentate, free, more or less as long as the cells. *Ovary* turbinate, densely hispid; style exserted; stigma simple.

Type: CAPE—3420 (Bredasdorp), (-AD) on Melkkamervlei farm in "Wasdam-se-kloof" on the South side of limestone hills but only seen on North-facing slopes and confined there to a small area 1/10/1972 *P. Uys* 1 (Holotype, NBG, isotypes STE, PRE). Limestone hills S. of Kathoek on the same farm, Oct. 1940, *N. S. Pillans* 9492 (BOL).

This species has only been collected twice and is probably local. It bears a superficial resemblance to *E. floccosa* in the section *Eurystoma* where it seems to be properly placed, but, on close inspection, there are apparently many important differences, e.g. the minute leaves, the shape of the corolla and the anthers, the hairy ovary and its apparent likeness or tolerance for limestone hills.

Erica vogelpoelii H. A. Baker, sp. nov. (Ericaceae-Ericoideae) Lamprotis.

Fruticulus erectus, gracilis, omnino, glaber. *Folia* 3—nata, 4 mm longa, leviter effusa, imbricata, linearia, subulata, vel anguste ovata, sulcata, mucronata, acuta. *Flores* terminales, in ramulis brevibus, pro parte maxima 3-nati, vel interdum fasciculati; pedunculi 5–6 mm longi; bractae secundae, medianae, parvulae, subsepaloideae. *Sepala* 5 mm longa, effusa obovata, concava, ad apicibus atrocarnata, scariosa, minute setociliata. *Corolla* 8 mm longa, anguste ovideo-urceolata, sicca, atrorosea, valido textura; lobi 2 mm longi, late effusi.

late ovati, atrorosei sed subsepalis nivea, obtusi, colorati similis corollae sed post maturitatem discolorescens. *Filamenta* filiformia; antherae inclusae, minus quam 1 mm longae, suboblongae, laterales, scabridulae, aerae, cristatae; poro fere pars dimidio lobi; cristae ad cellulis conjunctae, comparate grandes, varie laceratae, pallidae. *Ovarium* suboblongum, decrescens, substipitatum; stylo incluso; stigmatibus capitato.

An erect, slender, glabrous shrub to 45 cm or so. *Leaves* 3-nate, 4 mm long, slightly spreading, imbricate, linear-subulate to narrow ovate, sulcate, acute, mucronate. *Flowers* terminal on short branchlets, mostly 3-nate, but also in clusters of 6 flowers or so; peduncles 5–6 mm long; bracts two, median, very small and insignificant, subsepaloid. *Sepals* 5 mm long, spreading, obovate, concave, with black keel tips, coloured as corolla, scarious, minutely and sparsely setose-ciliate. *Corolla* c. 8 mm long, narrow-ovoid-urceolate, dry, strong in texture, deep rose-coloured but white under the lower part of the sepals; lobes 2 mm long, widely spreading, broad ovate, acute, concolourous with corolla at first but discoloured after maturity. *Filaments* filiform; anthers included, less than 1 mm long, obliquely oval, lateral, scabridulous, black, cristate, pore about 1/2 the cell; crests comparatively large and variously lacerate, fused to the lower part of the cell and only just protruding beyond the one side and the base, pallid. *Ovary* suboblong narrowing below and substipitate; style included; stigma capitate.

Type: CAPE—3419 (Caledon), (-DB). Growing in dense masses on the Bredasdorp mountains at c.610 m near the F.M. tower above Napier. Flowering period from December and probably through to April. 27/12/72 *L. Vogelpoel* 101 (Holotype NBG, isotypes STE, PRE). Also 27/1/73 from a population in the near vicinity but flowers much less mature, *L. Vogelpoel* 102.

This species was growing together with large populations of, inter alia, *E. melanacme* Guthrie & Bolus, *E. pulchella* Hoult, of many different shades of red and pink and also white, *E. irbyana* Andr., *E. multumbellifera* Berg. and *E. longifolia* Ait. This species is placed in the Section Lamprotis, where it clearly belongs, but is not very nearly related to any of those heretofore collected. The anther crests are very unusual if not unique.

Erica kougabergensis H. A. Baker var. ***recurvifolia*** H. A. Baker, var. nov.; A forma typica ita differt. *Folia* erecto-effusa vel subsquarrosa, oblanceolata vel anguste obovata, coriacea, crassa et ad apices incrassata, margine scariosis et crenatis dentibus caducis. *Sepala* ovato-lanceolata, margine aliquantum inflexis arte glandulosis, scariosa. *Corolla* cyathiformis; lobis continuis. *Antherae* a forma typica simulans sed interdum oblongae, obtusae, ad basibus bilobae, laevigatae, muticae; poro fere pars 2/3 lobi; *Stigma* peltato-capitellatum.

As the type but with the following differences: *Leaves* erect, recurved to squarrose, oblanceolate to narrow-ovate, thick, particularly at the apex, margins

scarious and with crenate teeth bearing caducous apical glands; *Sepals* ovate-lanceolate, the margins somewhat inflexed especially towards the apex and beset with viscid glands, glabrous, scarious. *Corolla* cyathiform, sometimes appearing viscid from the glands on the sepals; lobes continuous. *Anthers* as the type but occasionally forms have been collected with anthers oblong, obtuse, bilobed at the base, smooth, muticous; pore $2/3$ the length of the cell; *Stigma* peltate-capitellate.

Type: CAPE—3324 (Steytlerville) rock slopes on the Great Winterhoek Mts., Cockscomb (-DB) at c.1260 m, 2/2/1958, *Esterhuysen* 27491 (Holotype, BOL); 3/3/1957; *Esterhuysen* 27112; 30/11/1958; *Esterhuysen* 28017 (all in BOL); 17/9/50, *E. A. Archibald* 3489 (BOL), and the muticous specimens cited: 3323 (Willowmore), Rocky places Kouga Mt. near the peak (-DB), c.945 m, 27/10/1949, *Esterhuysen* 16237 (BOL).

Since this species was described a study of other undetermined material from the Section Pyronium has revealed collections that have been made in the Great Winterhoek Mts. on the Cockscomb feature that bear a close resemblance in structure to this species with some variations, particularly in the shape and set of the leaves which give it a different appearance. It is considered that these are not sufficient, when the variability of species in this section is considered, to merit a new species but a new variety is indicated, as is described above.

ACKNOWLEDGMENT

The author wishes to express his thanks to Dr. Louis Vogelpoel for collecting the type material of *E. vogelpoelii* and bringing it to his notice. It has been named in his honour for many reasons. Not only is he an exceptionally good collector, but he has made a study of growing ericas in captivity and has provided a great deal of material for the National Botanic Gardens at Kirstenbosch, where they have been grown under ideal conditions, thus helping to make a really first class erica garden.

I am also indebted to Mr. P. Uys for collecting the specimens of *E. uysii* which were taken to the Compton Herbarium and brought to my notice by Dr. Rourke. The species has, therefore, been named after Mr. Uys. Thanks are also extended to Dr. Rourke and Miss Esterhuysen for advice and assistance.

TRANSPORT OF RADIOACTIVE AUXINS IN THE SOUTH AFRICAN LABIATE, *IBOZA RIPARIA*¹

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ABSTRACT

Transport of the auxins, IAA, NAA and 2,4-D, was studied in stem sections of staminate and pistillate *Iboza riparia* and was found to be affected by sex, age and development of flowers. In young shoots, transport was rapid with a very short time delay prior to auxin efflux from the shoot sections. In older shoots, auxin efflux was retarded by several hours. The rate of transport was lowest at the time of flowering but recovered somewhat during subsequent weeks. Under some conditions the sexes differ appreciably in their ability to transport auxin.

UITTREKSEL

VERVOER VAN RADIOAKTIEWE OUKSIEN IN *IBOZA RIPARIA*, 'N SUID-AFRIKAANSE LID VAN DIE LABIATAE

Die vervoer van die ouksiene indool-3-asynsuur (IAS), naftalienasynsuur (NAS) en 2,4-dichlorofenoksiasynsuur (2,4-D) is in stingelseksies van meeldraad- en stamperdraende *Iboza riparia* bestudeer; dit is gevind dat dit deur geslag, ouderdom en ontwikkeling van die blomme beïnvloed word. Die vervoer in jong stingels is betreklik snel met slegs 'n baie kort tydvertraging voor uitskeiding van ouksien uit die stingelseksies. In ouer stingels, daarenteen, is ouksien-uitskeiding met 'n aantal ure vertraag. Die snelheid van vervoer is laagste tydens blomvorming maar neem in die daaropvolgende weke weer toe. Onder sekere toestande verskil die geslagte aanmerklik in hulle vermoë om ouksien te vervoer.

INTRODUCTION

Studies of auxin transport have progressed from qualitative descriptions of velocity, polarity and distribution in organs and whole plants to quantitative studies on kinetics and interactions of growth hormones and inhibitors, co-factors and conjugates involved in movement and metabolism of both endogenous and synthetic auxins (Fawcett, 1961; Kaldewey, 1967; Goldsmith, 1968, 1969; Thimann, 1969). Much of the present knowledge of auxin movement and metabolism was elucidated by work with *Coleus* (Jacobs, 1965, 1967), *Phaseolus* (Jaworski, Fang and Freed, 1955; McCready, 1963, 1968; McCready and Jacobs, 1963 a,b), *Helianthus* (de la Fuente and Leopold, 1970 a,b) and *Zea* (Scott and Wilkins, 1968, 1969; Wilkins and Scott, 1968).

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We decided to conduct our experiments with a South African labiate, *Iboza riparia*, and to give attention principally to questions of (a) changes in auxin transport during the period of an experiment, (b) the influence of shoot age on transport, and (c) the influence of shoot sex on transport.

There were several reasons for the choice of *Iboza*. The plant is related to *Coleus*, dioecious, readily propagated, and resistant to desiccation. *Iboza* shows conspicuous morphological differences between the staminate (male) and pistillate (female) plants. For example, stems of female plants are more glabrous than those of male plants, female plants also mature (flower) sooner than the males and their leaves are smaller and darker. However, examination of stem sections disclosed no internal anatomical difference between the sexes. The staminate flowers are somewhat larger than the pistillate. The flowers of both sexes are very small and pale lilac in colour and calyces are minute and campanulate in the two sexes. The ovary is four-lobed but is abortive in the staminate flower. The stamens number four; they are absent in the pistillate flower.

MATERIALS AND METHODS

Nine-cm long slips from clones of male and female *Iboza riparia* NE. Br. shrubs were grown into plants each with five to six internodes. All plants were topped at this stage to promote lateral shoot development and experiments were done with fourth internodes of lateral shoots, counting from the apex downwards. Each experiment was conducted with 15 mm sections from the same internode or, if that was not possible due to short internode length, a similar fourth internode from another shoot of the same plant was used, thus eliminating any minor physiological differences that might occur from plant to plant.

Agar block technique

The 15 mm sections were cut and placed in petri dishes on $5 \times 5 \times 2$ mm receivers of 3% w/v agar. Donor blocks were placed on top of the upright sections and a 10 μ l droplet of IAA-1- ^{14} C applied to each of the donors. At the termination of experiments, donor and receiver blocks were removed and placed in numbered scintillation vials, to which 2.0 ml of absolute ethanol had previously been added. When so required, sections were frozen and cut into 12 equal transverse subsections on a freezing microtome. The serial subsections were placed in scintillation vials containing 2.0 ml of absolute ethanol, ground finely with a glass rod, and 15.0 ml of Bray's (1960) liquid scintillation medium added. Donor and receiver blocks also were broken up with glass rods and 15.0 ml of Bray's medium added to the respective vials. Samples were counted for 10 minutes at 0°C in a Unilux II liquid scintillation spectrometer. Absolute dpm values were calculated on an Olivetti Programma computer.

U-Tube technique (Fig. A)

In preliminary experiments using agar blocks it was noticed that the amount of auxin obtained in receiver blocks fell off rapidly with shoot age, especially in female shoots. Since this effect might have been due to increased oxidative inactivation of auxin at the cut surfaces, it was thought that if the donor and receiver systems were aqueous, oxygen would be more effectively excluded from the cut surfaces. Consequently a U-tube apparatus was devised in which aqueous solutions at equal pressures could be maintained at each end of a shoot section. Donor and receiver parts were identical and consisted of L-shaped pieces of Pyrex glass tubing. Tubes with several internal diameters (from 4,5 to 7,0 mm) were made to accommodate stem sections of corresponding diameters. Long arms of the apparatus were ca. 5 cm and held upright; short arms were ca. 1 cm and held horizontally with the shoot sections sealed to and bridging the two short arms. The columns of donor and receiver solutions were kept at the same height.

Prior to cutting and waxing the stem section was blotted on tissue paper and then sealed in position with a low melting-point paraffin wax (40°C). Glass distilled water was pipetted into donor and receiver arms of the apparatus, care being taken that levels in donor and receiver arms were identical. The system was checked for leaks and allowed to equilibrate for 0,5 h prior to the addition of IAA-1-¹⁴C to the donor arm.

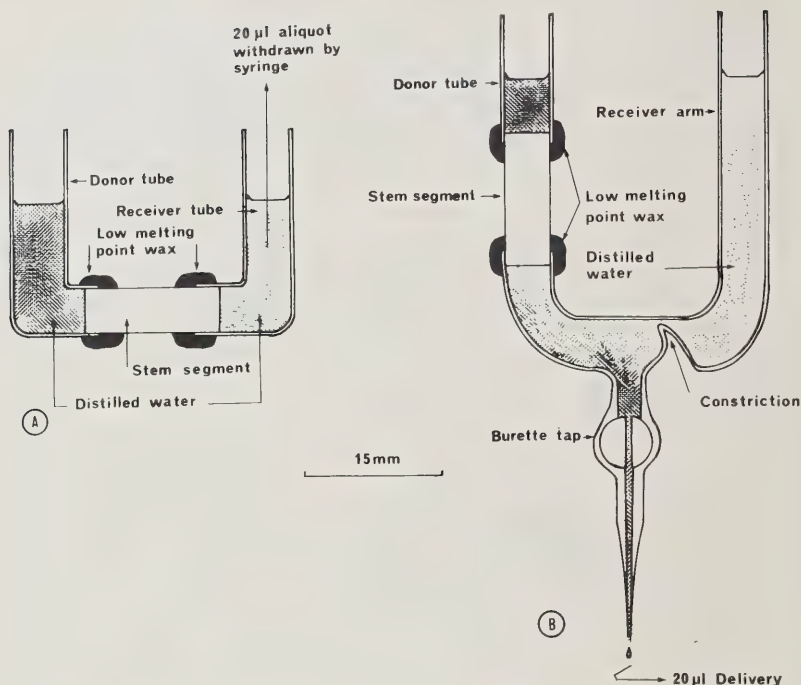
At preselected time intervals, a 200 µl sample was withdrawn from the receiver with a tuberculin syringe and re-injected rapidly, effectively mixing the auxin and the water. This process was repeated four times, after which a 20 µl sample was withdrawn from the bottom of the receiver with a 500 µl glass syringe. The 20 µl samples were dispersed into coded scintillation vials to which 15,0 ml of Bray's medium was subsequently added. Samples were counted and computed as described above. After withdrawal of each sample, 20 µl of glass-distilled water was added to the receiver to equalise the heights and therefore the pressures of the water columns.

Ringbarking technique

To obtain an indication of the amount of auxin moving in the xylem relative to that moving in the phloem and cortical layers, stem sections were ringbarked by excising a 2 mm wide ring of tissue 5 mm from either the apical or the basal end of the section. Care was taken to remove only the phloem and cortex and to expose the vascular cambium. The exposed tissues were then coated with paraffin wax and U-tube arms attached as described above.

Microburette technique (Fig. B)

To facilitate frequent sampling during the longer experiments the receiver arm of the U-tube apparatus was modified into a kind of microburette. This



FIGS. A and B.

Diagrammatic representation of U-Tube (Fig. A) and Microburette (Fig. B) set-ups used to determine radioactivity in aqueous samples.

was also a U-shaped vessel held upright and having a burette tap at the base between the two arms. The shoot section was waxed in place above the upright shoot section. The longer arm was filled with water to a level equal to that of the liquid in the donor tube.

Assembled microburettes were clamped to retort stands, the donor tube and receiver arm were filled with glass-distilled water, and the water levels equalised. A 0.5 h equilibration period was allowed prior to the application of a calculated volume of radioactive IAA, NAA or 2,4-D which, on assay, yielded equal dpm values.

The collection technique was as follows: 200 µl, ca. 10 droplets, were run out of each burette prior to collection of a 20 µl sample, i.e. the 11th drop, for liquid scintillation assay. The volume of the capillary tube above the

burette tap was designed to be approximately 200 μl . Collection of the 200 μl in a waste beaker reduced the sample numbers per experiment to one tenth of what otherwise would have been required, and still yielded a satisfactory estimate of the volume of ^{14}C in the burette and hence the rate of transport of the labelled auxin.

Auxin solutions

Labelled 3-indoleacetic acid-1- ^{14}C (IAA-1- ^{14}C), naph-1 yl-acetic acid-1- ^{14}C (NAA-1- ^{14}C), and 2,4-dichlorophenoxyacetic acid-2- ^{14}C (2,4-D-2- ^{14}C) were purchased from the Radiochemical Centre, Amersham.

The specific activities were as follows:

IAA-1- ^{14}C	: 57 mCi/mM (322 $\mu\text{Ci/mg}$),
NAA-1- ^{14}C	: 50,6 mCi/mM (270 $\mu\text{Ci/mg}$),
2,4-D-2- ^{14}C	: 29 mCi/mM (131 $\mu\text{Ci/mg}$).

The benzene solvents were removed under vacuum and the recrystallized auxins dissolved in absolute ethanol and diluted to 4 ml with sterile water (water-ethanol, 3:1 v/v). The stock solutions were kept in sterile, foil-wrapped injection ampules, and at no stage exposed to bright light. One ml of each of the solutions was withdrawn from the stock ampules with clean 1,0 ml glass tuberculin syringes, injected into sterile 10 ml rubber-stoppered ampules and diluted with glass-distilled water: absolute ethanol (9:1, v/v) to give approximately equal dpm values. Standards containing 10 μl of the diluted ^{14}C -labelled auxins were then withdrawn, injected into scintillation vials and 15,0 ml of Bray's scintillation medium added. Prepared samples were counted at 0°C and the results computed to an error of not more than 0,05%. The specific activities of the prepared samples were as follows:

IAA	: 2380,05 dpm/ μl (0,0322 $\mu\text{g}/\mu\text{l}$),
NAA	: 3544,95 dpm/ μl (0,0270 $\mu\text{g}/\mu\text{l}$),
2,4-D	: 3836,21 dpm/ μl (0,0131 $\mu\text{g}/\mu\text{l}$).

Computer technique

An Olivetti Programma P-101 was utilized to facilitate rapid calculation of the dpm per sample and the standard deviation of the count. A preset counting time of 20 min usually yielded a counting error of less than 1,5% in our experiments. In the initial experiments, in which finely ground tissue was used, the quenching effect of the tissue was determined and corrected for by computer.

RESULTS

Experiments using donor and receiver agar blocks

The first experiment was designed to give a general picture of the transport and distribution of applied auxin in an *Iboza* internode section over a 24 h

period. Sections from the fourth internode of 2-week old shoots of male *Iboza* were used in this experiment. The distribution of radioactivity was determined after 0,5; 1,0; 1,5; 7,0 and 24,0 h by cutting the original 15 mm sections into 12 equal subsections. Each part of the experiment was carried out in triplicate. The principal results are shown in Fig. 1 and Table 1. Results for the distribution of ^{14}C were plotted separately per time interval and irregularities in the curves smoothed out as follows: the mean activity recorded in subsections 1 & 2, 2 & 3, 3 & 4, and so on to 11 & 12, were totalled and the midpoint between each pair of these plotted, the nett result being that in the three dimensional figure all points are represented.

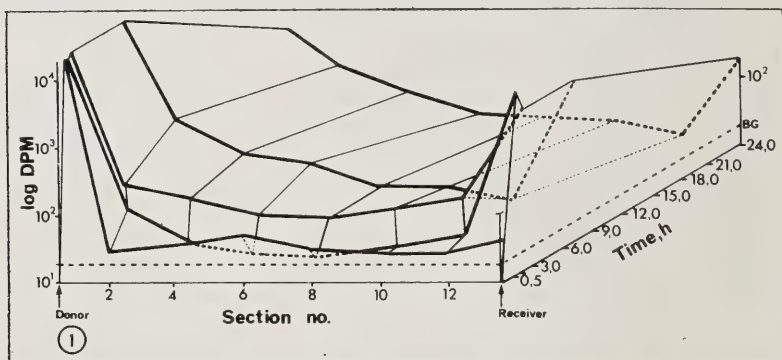


FIG. 1.

Basipetal distribution of radioactivity from IAA in 2-week male *Iboza* internode sections. Radioactivity was measured over a 24 h period in donor blocks, in receiver blocks and in 12 tissue subsections. The abscissae are plotted on a logarithmic scale. Note accumulation in the apical subsections and initial rapid transport indicated by high activity in receiver blocks with low activity in the central subsections. Accumulation of radioactivity within the section as a whole was appreciable after 1,5 h. Note also the gradual decline of activity in receiver blocks from 6 h onwards. BG, background count.

The data show an initial rapid movement of radioactivity throughout the section and into the receiver, the distribution being almost equal after 0,5 h. By the end of 1,0 h there was an appreciable accumulation in the receiver and an indication of accumulation in the apical subsections. By 1,5 h, ^{14}C accumulation in the section had increased markedly, but activity in the receiver had fallen from 7887 dpm at 1,0 h to 3980 dpm at 1,5 h. Radioactivity accumulated in the apical subsections up to 7 h but declined after that. Radioactivity in basal subsections declined after 1,5 h, whilst in receivers activity continued to increase from 3980 dpm at 1,5 h to 9946 dpm at 24 h.

TABLE I.
Distribution of basipetally-translocated radio-activity from IAA-1-¹⁴C in 15 mm sections from fourth internodes of 2-week male *Iboza* shoots.

Time ,h	DPM					Total
	Donor	Subsection number			Receiver	
		1	6	12		
0,5	28 332	57	60	50	62	28 561
1,0	21 460	189	28	58	7887	29 622
1,5	23 312	280	84	175	3980	27 831
7,0	21 157	1592	63	35	4977	27 824
24,0	17 340	890	46	49	9946	28 271

U-tube experiments

In these experiments sections from male and female shoots 4,5; 9,5 and 11,0 weeks old were used. Radioactive IAA was placed in the donor solution and the receiver solution was sampled at five-minute intervals up to 30 min. The results are summarised in Figs. 2 and 3 and Table 2. The most noteworthy feature of these results is the decline in transport with shoot age; with 11-week sections the rate was about one-third of what it was with the 4,5-week sections. Total counts for the male sections was 1159 dpm compared with 1173 dpm for the samples from the female sections. Table 2 indicates that by 9,5 weeks the total radioactivity recovered from the male shoot sections had dropped to 54% and the female to 61% of that recovered from male and female shoot sections aged 4,5 weeks, respectively. In shoot sections aged 11,0 weeks, the total radioactivity recovered had decreased to 33% of the 4,5 week totals. There seems to be an indication that the overall transport of auxin decreases with time more rapidly in the male shoot sections than the female, but it is evident that the efflux of auxin was more rapid in the male than the female shoot sections.

Thus there was a small but probably significant tendency for the male tissues to transport auxin more rapidly than the female tissues. This tendency is more clearly manifest in the results shown in Figs. 4 and 5 where the male sections have obviously transported more auxin than the female sections.

Comparison of IAA transport in intact and ringbarked male and female explants

In their studies of auxin transport in *Coleus*, Jacobs and McCready (1967) noted that there was no significant difference between the rate of transport by pith, and the rate by corner tissues which contain the xylem and phloem, even though the corner tissues had fewer, and larger cells in cross-section. We

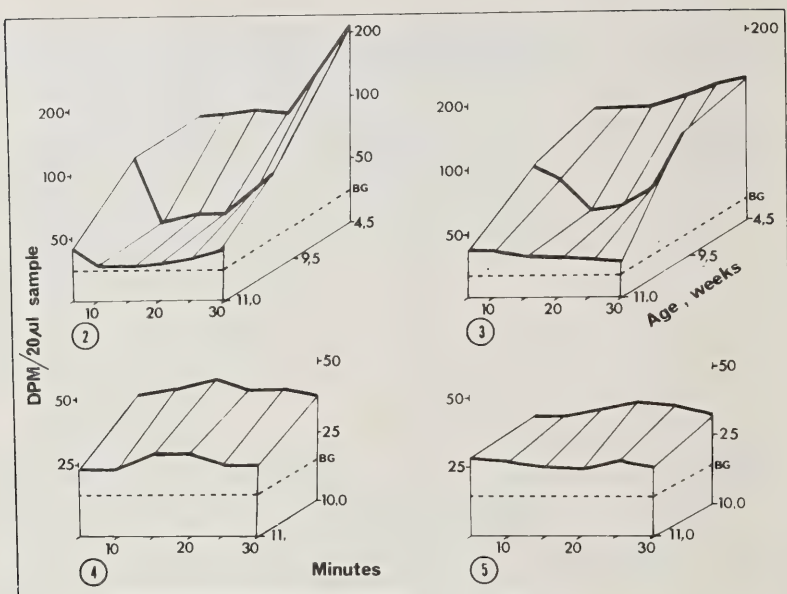


FIG. 2.

Time course of basipetal transport of IAA in male shoot sections as measured by the manometric method during a 30 minute period. The sections were taken from shoots 4,5; 9,5; and 11,0 weeks old. Note rapid decline in auxin transport with increasing shoot age. Data represent mean of six replicates. BG, background count.

FIG. 3.

Time course of basipetal transport of IAA in sections from female shoots aged 4,5; 9,5 and 11,0 weeks. Again note the rapid decline in the ability of the tissue to transport auxin with increasing shoot age. BG, background count.

FIG. 4.

Time course of transport of IAA in ringbarked sections from male shoots aged 10,0 and 11,0 weeks. Data represents mean of 10 sections. BG, background count.

FIG. 5.

As per Fig. 4 except that sections were from female shoots. Note that auxin transport through ringbarked female sections was lower than through ringbarked male sections. BG, background count.

were interested in conducting a related experiment with *Iboza* to determine if the aqueous donor and receiver system of the glass tubes might in some way permit a rapid movement through the xylem and thus lead to inaccurate interpretations of the transport system of intact plants. In this experiment sections from 10 and 11-week old male and female shoots were ringbarked 5 mm from

TABLE 2.
Accumulation of basipetally-translocated IAA-1-¹⁴C in receivers in 15 mm maleⁱ and femaleⁱⁱ shoot sections (from fourth internodes) of *Iboza*.

Age (weeks)	DPM		% DPM	
	Male	Female	Male	Female
4,5	615	603	100	100
9,5	338	371	54	61
11,0	206	199	33	33
Total	1159	1173		

i 23 replicates.

ii 21 replicates.

either the apical or basal ends. Transport of IAA was followed by the U-tube technique for a 30 minute period. The results are summarised in Figs. 4 and 5. No difference was found between the two positions of ringbarking; the points in the figures represent means of replicates of both positions. There was little change in transport during the course of this experiment. However the male sections transported appreciably more IAA than did the female sections.

To determine the relative efficiency of transport in the xylem/pith compared with the phloem/cortex, cross-sectional areas of twenty sections were measured. The relative areas are shown in Table 3: the xylem/pith area comprised 64% of the total. In the same table are shown the 30 min transport rates of the 10-week male and female sections. (Data from the 11-week sections were not included because the counts were very close to background levels.) The table shows that although the xylem/pith comprised 64% of the total area, those tissues transported only 44% in the male and 33% in the female of the auxin (transported by intact control sections). Thus the phloem/cortex appears to be considerably more efficient in transporting auxin than does the xylem/pith. The foregoing conclusion presumes that any wound effects were relatively minor as the experiment itself was not designed to exclude completely that possibility. However, from the work of others (e.g., Jacobs and McCready, 1967) such wound effects would appear to be small. For the present it is not possible to account for the seeming difference between our results, which showed much greater transport by phloem/cortex than by xylem/pith, and those of Jacobs and McCready (1967) which showed the same rate of transport by pith as by corner (xylem/phloem) tissues. Probably the explanation lies somewhere among the several differences in materials and methods employed in the two sets of experiments.

TABLE 3.
The effect of ringbarking on the rate of transport of IAA-1-¹⁴C in 10-week male and female *Iboza* shoot sections after a 30-min transport period.

	Relative cross-sectional area (%)	DPM		% DPM	
		Male	Female	Male	Female
Control (intact)	100	80	90	100	100
Xylem and pitch (ringbarked)	64	35	30	44	33
Phloem and cortex (by difference)	36	45	60	56	67

Microburette experiments

To gain further information on the decreased IAA transport in sections from older shoots the specially designed microburettes were used and the monitoring time was increased. The results of the first experiments, with sections from male and female shoots 12,5 weeks old and both basipetal and acropetal transport are shown in Fig. 6. They indicate that auxin transport is not a continuous, steady-state phenomenon, but consists of a phase of tissue loading, followed by a phase of increased auxin efflux up to a maximum (ΔT_{max}), and a sharply defined lag phase of transport during which the level of detectable ¹⁴C from the auxin decreased. With the female section, detectable ¹⁴C, although initially low (28 dpm) increased to 100 dpm at 1 h. Efflux of ¹⁴C remained static at ca. 100 dpm from 1 h to 3,5 h; thereafter the efflux increased rapidly to a ΔT_{max} at 5 h of 140 dpm. With the male section, auxin efflux increased gradually from 38 dpm at 0,5 h to 48 dpm at 0,8 h and to 80 dpm at 2,0 h. Maximum efflux, 185 dpm, was attained at 4,25 h. Thus in basipetal transport, the female differed from the male section in having a shorter tissue loading phase, a lower ΔT_{max} , and less total transport.

With acropetal transport ΔT_{max} was not sharply defined for either sex. Both curves showed a low plateau of transport of about 2 hours. However the data suggest that the transport rate falls off earlier in the female than in the male. With young, 3-week sections (Fig. 7), there was little evidence of a tissue loading phase. Maximum efflux, 1350 dpm, was reached at 3,0 h followed shortly by a lag phase with a ten-fold decrease. In contrast the sections from 15-week shoots showed little change in transport during the eight-hour experimental period and little difference between the acropetal and basipetal directions of transport.

Comparisons of IAA, NAA and 2,4-D transport in male and female stem sections

At this stage sufficient evidence was at hand to justify the investigation of synthetic auxins. Experiments on basipetal transport of IAA-1-¹⁴C, NAA-1-¹⁴C

and 2,4-D-2-¹⁴C through male and female sections aged 17 and 22 weeks were conducted using the microburette technique. The results are summarised in Figs. 8–11.

Correlated with visible development of the inflorescence in female plants, auxin efflux changed markedly between weeks 15 and 17 (Figs. 7, 9). At week 15 basipetal transport in the female section was essentially similar to acropetal transport in the male (Fig. 7). However, by week 17 basipetal transport of IAA in both males and females attained ΔT_{maxima} by 8 h after time delay periods of from 4 to 6 h (Figs. 8 and 9).

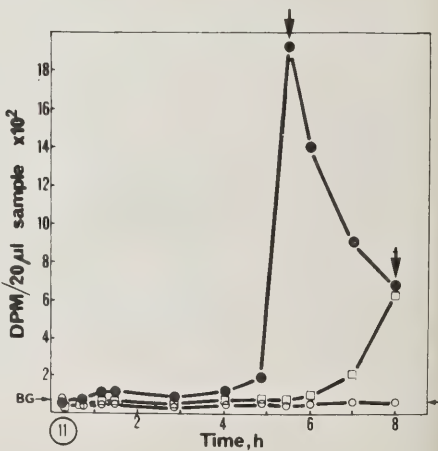
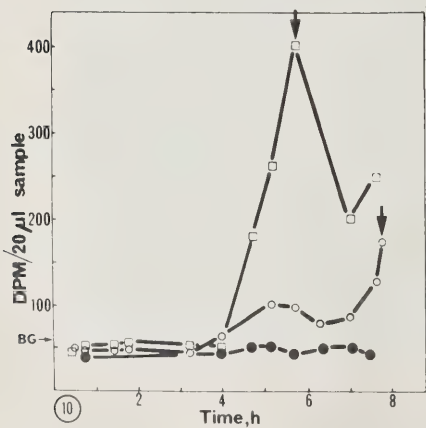
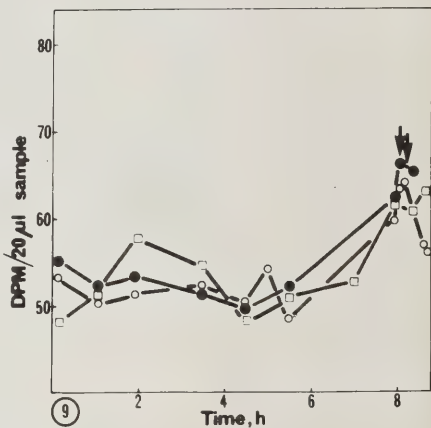
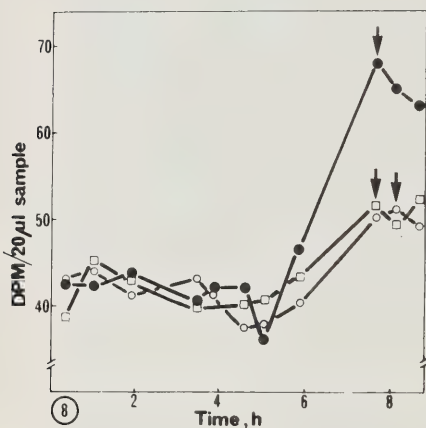
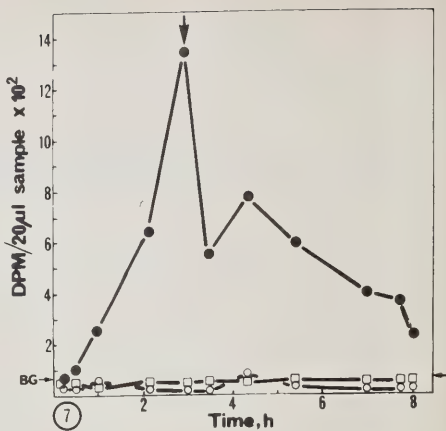
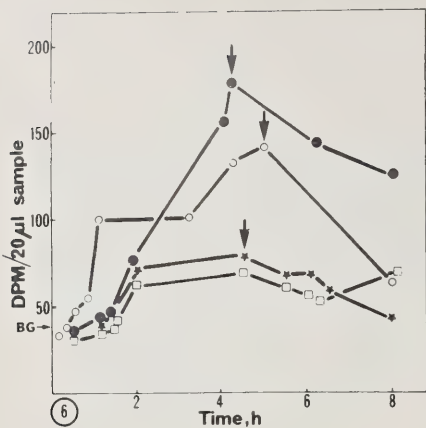
The transport patterns of IAA and 2,4-D showed similar trends (Figs. 8 and 9); however 2,4-D was transported to a greater extent than either NAA or IAA in both male and female sections.

Between week 17 and week 22 formation of flowers by female plants ceased, and correlated with this was a marked increase in the rate of auxin transport, more so in female than in male sections (Figs. 10 and 11). Of interest is the difference between male and female sections in the rate of transport of radioactivity from 2,4-D. In the male section transport remained static at ca. 50 dpm/sample. In the corresponding female section, 2,4-D transport increased to 110 dpm at 1.5 h, and after 4 h rose steeply to a ΔT_{max} at 5.5 h of 1897 dpm. Both male and female sections showed a prolonged tissue loading phase with IAA and NAA. In the male sections transport of both these auxins reached maxima shortly after 5 h, then declined, and then rose again and was still rising at the termination of the experiment. In the female sections transport of IAA and NAA did not reach maxima but the rates were rising sharply at termination.

DISCUSSION

The results of the experiments with *Iboza* stem sections on the uptake, distribution and efflux into receivers of radioactivity from IAA-1-¹⁴C, NAA-1-¹⁴C and 2,4-D-2-¹⁴C indicate that auxin transport is NOT a steady-state phenomenon in this plant. Figure 1 showed that between 1.0 and 1.5 h radioactivity from IAA increased and reached a maximum in the section at 7.0 h, and then declined. Rapid accumulation in the receiver during the first hour, coupled with low activity in stem sections is probably the result of a high rate of transport. The decrease in receiver activity during the period 1.0 to 1.5 h suggests that a major portion of the transportable auxin pulse has, by this time, moved out of the tissue section and that accumulation of IAA or its metabolites has commenced. Maximum accumulation of IAA or its metabolites within the apical portions of the shoot sections occurred between 1.5 and 7.0 h.

The effect of shoot age on the decline in auxin transport is demonstrated in Figs. 2, 3, 6 and 7. The data of Figs. 6–11 show that the time taken to pre-



load the sections with exogenous auxin prior to efflux, increases with shoot age. The reasons for the decrease in basipetal transport of auxin with shoot age are not clear. Possibly there is a decrease in the availability of transport sites within the section as a consequence of ageing or of the physiological changes associated with flower formation.

Naqvi and Gordon (1965) with *Coleus* found a decrease in the ratio of basipetal to acropetal transport from 3.0 to 1.3 in non-flowering and flowering plants. Our results also showed that flowering affects the rate of transport of auxin (see Figs. 6–11). Although flowers were not formed in male plants, suppression of auxin efflux was most marked at week 17, the time of female flowering (Fig. 8). In 22-week female shoots (Fig. 11) flower formation had ceased and this was marked by a strong rise in radioactive efflux. Similar results were obtained in 22-week male sections (Fig. 10).

The microburette technique proved very convenient for determining the efflux of auxins from stem sections. Experiments using this technique showed that the time-delay factor (Kaldewey, 1967) increased with shoot age. With *Iboza* in most instances, an increased transport of radioactivity followed the

FIG. 6.

Transport of radioactivity from IAA in sections from male and female shoots aged 12.5 weeks, indicated as follows: basipetal, male (●—●) and female (0—0); and acropetal, male (□—□) and female (*—*). BG, background count. Note that basipetal transport rate in male sections is higher than in the corresponding female sections. $\downarrow$, Δ^T max.

FIG. 7.

Transport of radioactivity from IAA in sections from 3.0 week male shoots and 15.0 week male and female shoots, indicated as follows: basipetal, 3-week male (●—●); acropetal, 15-week male (0—0); and basipetal, 15-week female (□—□). BG, background count. Basipetal transport in sections from 3-week male shoots increased after 0.28 h, whereas no real change in transport was found with either the 15-week male or female shoots. A 10-fold decrease in activity occurred after Δ^T max in 3-week male shoots.

FIG. 8.

Comparison of basipetal transport of IAA (0—0), NAA (□—□) and 2,4-D (●—●) in sections from male shoots aged 17 weeks. Note higher rate of transport of 2,4-D and the longer time delay from 0.28 h (Fig. 7) to 5.0 h (this Fig.), prior to detection of significant increases in auxin efflux. Background not inserted due to low activity of the samples.

FIG. 9.

Comparison of basipetal transport of IAA, NAA and 2,4-D in sections from female shoots 17 weeks old. Symbols as for Fig. 8. Note the very long time delay prior to an increase in ^{14}C -efflux and the attainment of Δ^T max. Background not inserted due to very low activity of the samples.

FIG. 10.

Comparison of basipetal transport of IAA, NAA and 2,4-D sections from male shoots 22 weeks old. Symbols as in Fig. 8. Note the terminal rise in efflux with IAA and NAA following the decline from Δ^T max.

FIG. 11.

Comparison of basipetal transport of IAA, NAA and 2,4-D in sections from female shoots 22 weeks old. Symbols as in Fig. 8. Note that IAA and NAA effluxes were rising at the termination of the experiment, and the much earlier and greater efflux of 2,4-D in this experiment.

time-delay factor. After attainment of maximum transport ($\Delta T_{\max}$) efflux declined. That age and sex influence the amount of auxin transported is clear from Figs. 6–11. For example, in 3-week male sections $\Delta T_{\max}$ was attained at 3 h (Fig. 7) while in 12,5-week male sections $\Delta T_{\max}$ was not attained until 4,5 h (Fig. 6). Similar differences also appeared between the sexes (e.g. Fig. 10, 11). Wilkins (Personal communication) suggested that the position of $\Delta T_{\max}$ would be influenced also by temperature. However, this would not have been a factor in our experiments as temperature was kept constant at 22°C.

Of major importance is the rapid decline in the amount of radioactivity from the applied auxin after attainment of $\Delta T_{\max}$, which in *Iboza* occurred within 0,5 h of attainment of $\Delta T_{\max}$. This confirms the results of dela Fuente and Leopold (1970 a, b, c) who found that the half-life of the transportable pool of auxin was about 0,5 h in 10-day *Helianthus* seedlings. It is noteworthy that we confirmed their results utilizing quite different techniques.

Toward the end of our investigation we conducted a few preliminary experiments with paper chromatography to examine the possibility that a portion of the applied auxins might be conjugated in the *Iboza* tissues. The results suggested that by seven hours indoleacetyl aspartate (IAAsp) comprised 38 per cent of the radio-activity in the extracts of 12, 5-week stem sections. The formation of IAAsp by the conjugation of exogenous IAA with aspartic acid in peas was reported earlier by Andreae and Good (1957). This and related compounds have also been detected in other plants (Good, Andreae and Van Ysselstein, 1955; Andreae and Van Ysselstein, 1955; Robinson, Forman and Addicott, 1968). In general plant tissues appear to require a two-hour induction period for the formation of IAAsp, with maximal conjugative activity in four to six hours (Andreae and Van Ysselstein, 1960; Zenk, 1964). In *Iboza* maximal conjugation of exogenous auxin appears to coincide with the decline in the transport of the auxin. Chromatograms of NAA-1-¹⁴C and 2,4-D-2-¹⁴C from stem extracts indicated that conjugation of these auxins also takes place in *Iboza*, but as yet the metabolites have not been identified.

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STUDIES IN THE GENERA OF THE *DIOSMEAE* (RUTACEAE): 2. *EUCHAETIS GLABRA* WILLIAMS SP. NOV.

ION WILLIAMS

(*Compton Herbarium, Kirstenbosch*)

ABSTRACT

A new species of *Euchaetis* from the Hottentots Holland Mountains in the South Western Cape is described.

UITTREKSEL

STUDIES VAN DIE GENERA VAN *DIOSMEAE* (RUTACEAE): 2 *EUCHAETIS GLABRA* WILLIAMS (SP. NOV.) Een nuwe *Euchaetis* soort vanaf die Hottentotshollandberge in die Suidwes Kaap is beskryf.

***Euchaetis glabra* Williams, sp. nov.** propria propter folia orbiculares marginibus tenuibus, totam plantam glabram.

Frutex ad 50 cm, paulo diffusa, ad basim 20 cm monocaulis. *Ramuli* erecti, glabri, graciles, dense foliosi. *Folia* c. 4 mm longa, 2,5 mm lata, petiolata, orbiculata vel elliptica, obtuse rubro-callosa, glabra, sub-succulenta, marginibus hyalinibus, tenuibus, minute serrulatis. *Inflorescentia* terminalia ± 12 aggregata, involucribus conspicuis carentibus. *Bractea* 1, folium simulans. *Bracteolae* duae ad basim pedicello, 3 mm longae, 1 mm latae, minute rubro-callosae, paulo clavatae, glabrae, minute ciliolatae. *Sepala* 5, 2,5 mm longa, 1,3 mm lata, oblonga, obtusa, minute ciliolata. *Petala* 5, 4 mm longa, 1,4 mm lata, oblanceolata, obtusa, transverse barbata, unguibus sparsim ciliatis. *Staminodia* 5, vestigialia. *Fila* 5, glabra, post anthesin 1,3 mm longa. *Antherae* 5, ante anthesin 0,8 mm longae, 0,6 mm latae, oblongae, roseae, apicibus minute glandulosi. *Pollen* 45 μ longum, 18 μ diam., oblongum. *Discus* ovarium excedens, ruber. *Stigma* capitatum. *Stylus* glaber, 1 mm longus. *Ovarium* 5-carpellatum, 0,7 mm diam., glabrum. *Fructus* 5-carpellatus, 4,5 mm longus, 5 mm diam., glaber, cornibus perbrevis. *Semen* 3,5 mm longum, 2 mm latum, piceum, nitens.

Type: CAPE—3418 (Simonstown). On a N.E. ridge of the Kogelberg (-BB), 5,3 km due south of Sir Lowry's Pass summit, Caledon Division, *Williams 1654* (NBG, holotype; PRE, STE, K, MO, M, S, isotypes).

This is a species new to science discovered by Miss E. Esterhuysen of the Bolus Herbarium who collected it in July 1940 near the summit of Rooskraalberg, a mountain to the east of Moordenaarskop in the Hottentots Holland Mountains.

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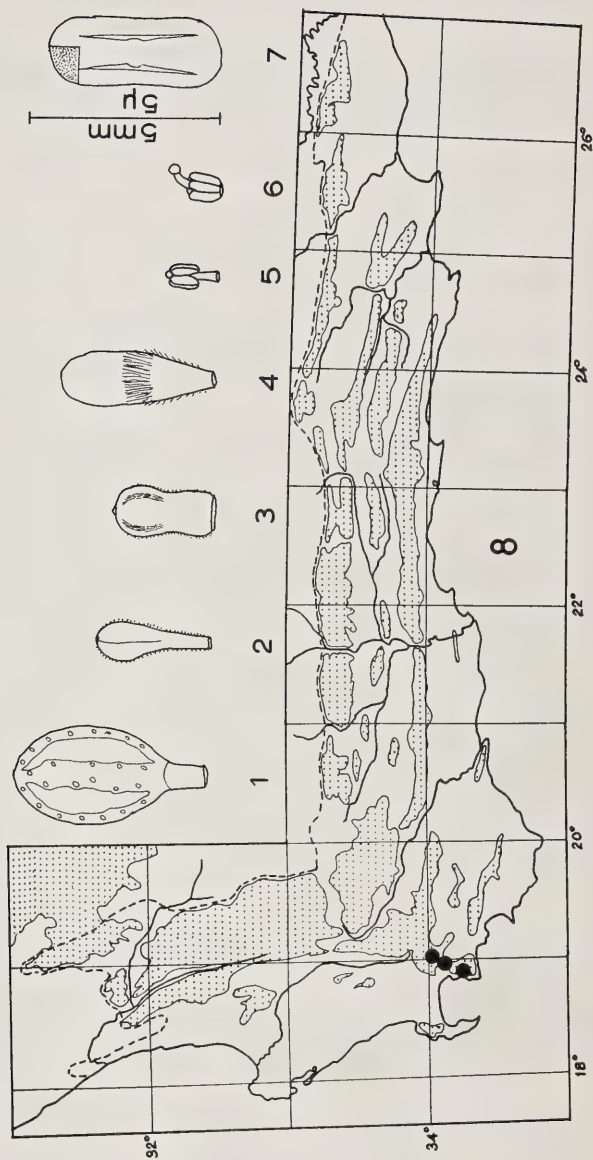


FIG. 1.
Euchaetis glabra: 1, leaf. 2, bracteole. 3, calyx lobe. 4, petal. 5, anther. 6, gynoecium. 7, pollen.
 8, distribution.

Shrubs up to 50 cm tall, somewhat diffuse, the lower 20 cm single stemmed, erect, ringed with horizontal leaf scars, about 5 mm diam. *Branches* normally arising in clusters, soon leafless, glabrous, fairly erect. *Branchlets* erect, slender, glabrous, densely foliate. *Leaves* about 4 mm long, 2,5 mm broad with a petiole about 1 mm long, orbicular or elliptic, obtuse with a blunt reddish callus, glabrous, somewhat fleshy, gland dotted near the margins and midrib, hyaline margins thin and minutely serrulate. *Inflorescence* terminal, with the florets, about 12 in number, opening at different times; there are no conspicuous involucre leaves. *Bract* leaf like, one in number subtending each floret. *Bracteoles* 2, 3 mm long, 1 mm broad, somewhat club shaped, obtuse, glabrous, ciliolate, somewhat keeled, apex with a small blunt reddish callus. *Calyx lobes* 5, 2,5 mm long, 1,3 mm broad, oblong, obtuse, thickened towards the apex, hyaline margins minutely ciliolate, tinged with red. *Petals* 5, 4 mm long, 1,4 mm broad, oblanceolate, obtuse, gland dotted, transversely bearded, with the *claw* sparsely ciliate, translucent, narrowing evenly to the base. *Staminodes* 5, about 0,1 mm diam., vestigial, a minute spherical gland on the disc. *Filaments* 5, at first about 0,5 mm long, lengthening to 1,3 mm long after anthesis and carrying the discharged anthers to the outside of the petals, glabrous. *Anthers* 5, before anthesis 0,8 mm long, 0,6 mm broad, oblong, reddish, with a minute spherical gland about 0,15 mm diam. at the apex; under X 16 magnification the surface of the anther is seen to be roughened with red glands on an orange background. *Pollen* 45 μ long, 18 μ diam., oblong, slightly narrowed in the middle, surface rough-dotted and with three longitudinal striations. *Disc* slightly exceeding the ovary, dark red in colour, exuding nectar. *Stigma* capitellate, at first inclined. *Style* glabrous, becoming 1 mm long. *Ovary* 5-carpellate, 0,7 mm diam., glabrous. *Fruit* 5-carpellate, 4,5 mm long, 5 mm diam., glabrous, surface translucent and gland dotted; *horns* very short. *Seed* 3,5 mm long, 2 mm broad, black, shining.

SPECIMENS EXAMINED

CAPE—3418 (Simonstown): (-BB) Rooskraalberg, swamp near summit 3 000', -/7/1940 *Esterhuysen* 2642 (BOL, SAM, NBG); Moordenaarskop, summit 4 400', 3/10/1943 *Esterhuysen* 9129 (BOL, NBG); Moordenaarskop, swamp on W. side, 4 000', 6/8/1950 *Esterhuysen* 17399 (BOL), 10/5/1969 *Stehle* TS48 (STE); Kogelberg, summit, 4 100', 19/2/1966 *Rourke* 313 (NBG); N.E. end of Kogelberg Mts., 2 650', 10/6/72 *Williams* 1654 (NBG, PRE, STE, K, MO, M, S), 12/5/1970 *Boucher* 1263 (STE). CAPE—3419 (Caledon): (-AA) plateau between Victoria Peak and Dwarsberg, streamside, 3 000–4 000', 15/10/1950 *Esterhuysen* 17739 (BOL, NBG); Dwarsberg, Jonkershoek, 3 500', 24/6/1958 *Rycroft* 2125 (NBG); swampy plateau between Victoria Peak and head of Jonkershoek valley, 3 000', 19/1/1948 *Esterhuysen* 14382 (BOL); along path to Victoria Peak, 4 000', 12/6/1958 *Esterhuysen* 27792 (BOL).

DISTRIBUTION AND BIOLOGY

Euchaetis glabra is confined to a fairly small area, about 22 km from north to south, in the Hottentots Holland Mountains of the s.w. Cape. It is found at altitudes ranging from 800 to 1 340 m (2 650 to 4 400 feet) above sea level growing in dampish soil, in swampy places and along stream sides, in fairly dense stands dispersed amongst slender restios. It appears to have a rather extended flowering period, the type collection, made in June, having both fruiting and flowering heads. Furthermore the florets in a single head are found to be in all stages of flowering. Pollination appears to be effected by small insects. In the early stages of flowering the style is bent to one side, and it only becomes erect at a later stage when the anthers, having shed their pollen, are withdrawn from the centre of the floret. Self pollination would therefore seem to be made impossible. When ripe, the seeds, as is normal in the *Diosmeae*, are ejected by a catapult mechanism and may be thrown a distance of a few feet from the parent plant. Regeneration takes place after fires. The plant has a pleasant odour when crushed, reminiscent of aniseed.

DISCUSSION

As far as can be seen from the present state of my knowledge of *Euchaetis*, all species in the genus have the following characters in common. (1) The *flowers* are normally aggregated into multiflorous heads; the number varying from 3 to 60. (2) The *petals* are transversely bearded in the vicinity of the throat of the flower. (3) *Staminodes* are virtually absent usually being represented by a vestigial gland about 0,05 to 0,10 mm in diameter. (4) The *anther* invariably possesses a minute gland at the apex. (5) The *disc* is well developed and equals or exceeds the ovary. (6) The *stigma* is capitate. (7) The *style* is short, never more than 2 mm long. (8) The *filaments* and *style* are glabrous. (9) The *ovary* is 5-carpellate. (10) The *fruit* is short-horned at the summit. The length of the horn in most cases being less than 1,5 mm.

As the species above described complies with the above criteria, I have no hesitation in assigning it to the genus *Euchaetis*. Bartl. & Wendl.

Euchaetis glabra is recognised as distinct on account of its having orbicular-elliptic petiolate leaves with thin margins and in its being a completely glabrous plant.

A NEW SPECIES OF *SALSOLA*

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ABSTRACT

A new species, *Salsola verdoorniae* from the south-eastern Little Karoo, is described here.

UITTREKSEL

'n NUWE *SALSOLA* SOORT

Salsola verdoorniae, 'n nuwe spesies van die suid-oostelike dele van die Kleinkaroo, word hier beskryf.

Salsola verdoorniae Toelken sp. nov. ab speciebus austro-africanorum foliis caulum lateralium distichis differt.

Fruticuli caulibus prostratis tortuosis lignosis usque ad 25 cm longis et 0,5-1 cm diametro ad basim, ramossissimi, pulvinos irregulares formantes, internodiis 0,3-0,6 cm longis et tomentosis in caulibus principalibus et foliis spiraliter dispositis, foliis caulum brevium lateralium distichis. *Folia* alterna, 2-3,5 mm longa, 1-2 mm lata, acuta, amplexicaulia, dorsale carinata praecipue in caulibus lateralibus, tenacia et leviter succulenta ad basim, dense tecta pilis adpressis, cano-viridia. *Flores* axillares et bracteis duobus ovatis carinatis 2-2,5 mm longis et dense tectis pilis adpressis. *Tepala* triangularia vel lanceolata, 2,5-3,5 mm longa, dense tecta pilis adpressis. *Stamina* 2 mm longa, antheris anguste lanceolatis 1,2-1,5 mm longis et connectivis apices obtuses formantibus, lobis oblongis succulentis inter stamina. *Gynoecium* stylo c. 1 mm longo et stigmatibus bifido 0,5-0,8 mm longo.

Type: CAPE: 3321 (Ladismith): Springfontein (-CC), *Tölken 1656* (BOL, holo!).

Shrublet with prostrate, tortuous woody branches up to 25 cm long and 0,5-1 cm in diameter towards the base, much branched forming a dense mat between the gravel, with internodes 0,3-0,6 cm long and tomentose on the main branches and with leaves spirally arranged, producing short axillary branches with no internodes visible between the leaves which are arranged strictly in two ranks. *Leaves* alternate, 2-3,5 mm long, 1-2 mm broad, sharply acute, dorsally keeled especially on the short axillary branches, amplexicaule, tough and slightly fleshy towards the base, densely covered with adpressed hairs, grey-green. *Flowers* axillary with two ovate keeled bracts 2-2,5 mm long and densely covered with adpressed hairs. *Stamens* 2 mm long, with narrowly lanceolate anthers

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1,2–1,5 mm long, with the connective forming an obtuse apex and with oblong fleshy lobes between the stamens. *Gynoecium* with style c. 1 mm long and with bifid stigma, 0,5–0,8 mm long.

S. verdoorniae grows on, or in association with, areas covered with quartzite gravel, but it occurs only in a few such localities just north of the Langeberg mainly between Barrydale and Muiskraal.

Two localities, i.e. on the farms Springfontein and Brandrivier have been revisited repeatedly during the past five years, but flowers were found only once after a good rain in 1968. This might account for the few times that the plant has been collected and no flowers have been seen previously.

C. A. Smith gave this species the manuscript name of *S. eragrostoides* referring to the similarity of the axillary branches to the ears found in the genus *Eragrostis*. It must, however, be pointed out that leaves are only two ranked on the axillary branches, while they are spirally arranged on the main branches and, therefore, this name could be misleading. However, it would be appropriate to name this distinct species in honour of Dr. I. C. Verdoorn, who has done so much towards the understanding of the taxonomy of this intricate genus in Southern Africa.



FIG. 1.

S. verdoorniae in its habitat (coin 1,5 cm in diameter)

**'N EMBRIOLOGIESE ONDERSOEK VAN *ROMULEA ROSEA* ECKL.
VAR. *REFLEXA* BEG.***

2. Die ontwikkeling van die endosperm, embrio en saadhuid.

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UITTREKSEL

In die saadknop van *Romulea rosea* Eckl. var. *reflexa* Beg. word nukleêre endosperm gevorm. 'n Endospermhaustorium vernietig die oorblywende chalazale nucellusweefsel. In die ryp saad is die endosperm horingagtig en ryk aan proteïene en olie. Die embrio-ontwikkeling stem ooreen met die *Sagittaria*-variasie van die Caryophyllaceae-tipe. Die saadhuid word oorwegend van die buitenste integument gevorm. Die resultate van die ondersoek word vergelyk met die van Ferraris (1902) en Béguinot (1907) wat *R. bulbocodium* en *R. columnae* ondersoek het. Die embriologie van *Romulea* en *Crocus* word ook vergelyk.

ABSTRACT

THE EMBRYOLOGY OF *ROMULEA ROSEA* ECKL. VAR. *REFLEXA* BEG. 2. DEVELOPMENT OF THE ENDOSPERM, EMBRYO AND SEED COAT.

Nuclear endosperm is formed and an endosperm haustorium absorbs the remaining nucellar tissue. The ripe seed has a horny endosperm which contains protein and oil. The embryo in its development belongs to the *Sagittaria* variation of the Caryophyllaceae type. The seed coat is formed mainly by the outer integument.

The present results are being compared with those of Ferraris (1902) and Béguinot (1907) who have investigated *R. bulbocodium* and *R. columnae* and an embryological comparison of *Romulea* and *Crocus* is given.

INLEIDING

Die anatropse saadknop van *Romulea rosea* Eckl. var. *reflexa* Beg. het twee integumente waarvan die buitenste meerlagig is en die binneste die mikropielkanaal vorm. Die volwasse saadknop is tenuinucellaat omdat die monospore, agtkernige embriosak die nucelluskap van die jong saadknop vernietig. Onder die hipostase wat 'n pilaartjie vorm waarop die antipodes gedra word, is die chalazale nucellusweefsel nog aanwesig (Steyn, 1973).

Gedurende bevrugting word een sinergied deur die groeiende stuifmeelbuis vernietig. Die bevrugte eiersel lê langs die oorblywende sinergied, terwyl die sekondêre embriosakkern bokant die verdwynende antipodes aangetref word (Steyn, 1973).

Die bou en ontwikkeling van die saadknop van *R. rosea* var. *reflexa* stem in breë trekke ooreen met die van die twee Suid-Europese soorte, nl. *R. bulbocodium* en *R. columnae* wat deur Ferraris (1902) en Béguinot (1907) ondersoek is.

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* 'n Verkorte weergawe van 'n deel van 'n verhandeling goedgekeur vir die graad Magister in die Natuurwetenskappe aan die Universiteit van Stellenbosch.

MATERIAAL EN METODEDES

Soos in die vorige ondersoek is blomme, vrugte en sade in F.A.A. gefikseer, in was ingebed en mikrotroomsneë gemaak en gekleur met anilienblou en hematoksilien (Steyn, 1973).

ONDERSOEK

Vorming van die endospermweefsel.

Tiperend van 'n groot, wye embriosak ($1\ 000\ \mu\text{m} \times 500\ \mu\text{m}$) word nukleêre endosperm by *Romulea rosea* var. gevorm. 'n Groot aantal klein ($8,5\ \mu\text{m}$) vrye kerne word egalig versprei in die wandstandige sitoplasma van die embriosak (fig. 8). Die sitoplasma konsentreer rondom die embrio waarin die buitenste selle reeds periklinaal deel, en rondom die hipostase waar die antipodes verdwyn het.

Wanneer die kerne ongeveer $30\ \mu\text{m}$ uitmekaar is, word 'n tweede lagie kerne aan die vakuoolkant van die embriosak gevorm en selwande ontstaan nou tussen die delende kerne. Die jong, plat selle verleng hoofsaaklik radiaal en is dunwandig en gevakuoleerd. Die embriosak word in 'n middelpuntsoekende rigting laag vir laag opgevol met dunwandige selle.

Weens die vergroting van die saadknop, raak die buitenste selle radiaal gestrek en verdeel hoofsaaklik periklinaal om meer konsentriese lae endospermselle te vorm. Wanneer die saadknop sy maksimum grootte bereik het, verdik die selwande en kleur helderblou met anilienblou wat aandui dat kallose aanwezig mag wees (McLean & Ivimey-Cook, 1941). Schultze se oplossing of jodium en swawelsuur gee 'n rooibruin reaksie maar korallienoplossing (McLean & Ivimey-Cook, 1952) het geen uitwerking op die selwande nie.

In die ryp saad bevat die endosperm 'n ryk proteïen- en olie-inhoud. Die selkerne is nog sigbaar. Die selwande is horingagtig, baie verdik (fig. 10) en anisotroop.

Ontwikkeling van die endospermhaustorium

Na bevrugting vergroot die saadknop vinnig. Aan die begin van endospermvorming verdeel die selle van die binne-integument naby sy aanhegting aan die chalaza, regoor die hipostase. Lg. breek af aan sy basis en word weggestoot na die kant van die embriosak. Die buite-epidermisselle van die binne-integument regoor die verdwene hipostase verleng radiaal tot byna vyfmaal hul oorspronklike hoogte, sodat die binne-integument inbuig rondom die basis van die embriosak en 'n ringvormige vernouing hier vorm (fig. 1). Die oorblywende chalazale nucellusweefsel lê onderkant hierdie vernouing. Die onderpunt van die embriosak vorm nou 'n voet met 'n plat basis en verdikte wand.

Aan die embriosakkant van die voet konsentreer die sitoplasma en die endospermkerne is hier opvallend groot en ellipties of gelob, met twee tot

minstens tien nukleoli. Op geen stadium kan selwande in die poliploïede embriosakvoet onderskei word nie. Die endospermweefsel begin aan die bokant van die voet (fig. 1).

Hierdie struktuur word as 'n endospermhaustorium beskou wat die oorblywende nucellusweefsel vernietig totdat daar net drie tot vier platgedrukte sellae in die chalazale wyk oorbly. Wanneer die embriosak gevul is met dunwandige endospermweefsel, verdwyn die poliploïede kerne maar die sitoplasma bly oor en kleur baie donker (fig. 1).

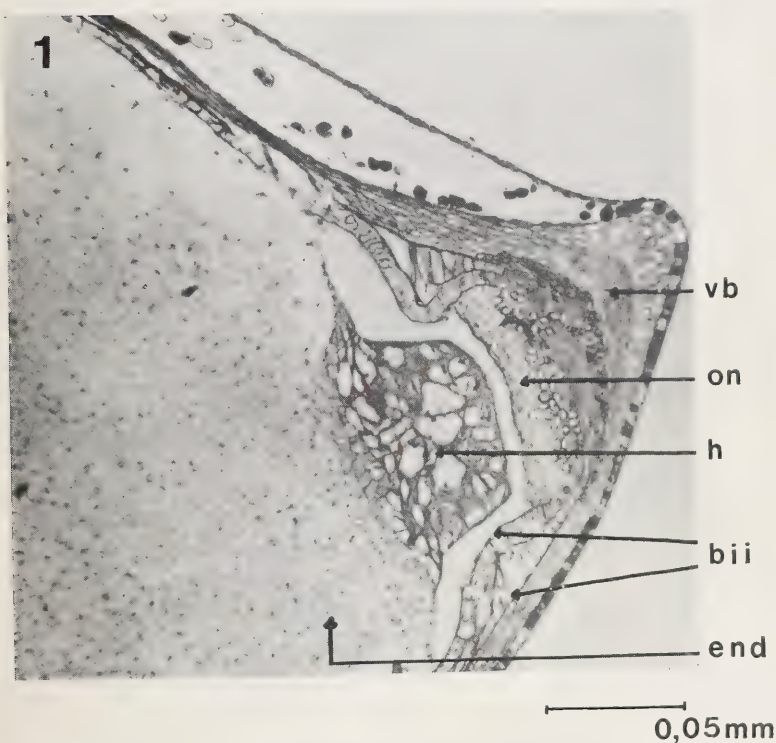


FIG. 1.

Foto van 'n lengtesnee deur die saad van *Romulea rosea* var. *reflexa* om die endospermhaustorium aan te toon: bii, binne-integument; end, endospermselle; h, haustorium; on, chalazale nucellusweefsel; vb, vaatbondel van die chalaza.

Ontwikkeling van die embrio

By *Romulea rosea* var. vind die eerste verdeling van die sigoot relatief vroeg plaas, wanneer daar nog maar min vrye endospermkerne gevorm is.

Twee ongelyke selle word deur 'n dwarsdeling van die sigoot gevorm: 'n groot, gevakuoleerde basale sel (cb in fig. 2), en 'n klein byna lensvormige, sitoplasmaryke apikale sel (ca in fig. 2). Die basale sel deel nie verder nie, maar vergroot om 'n eensellige, sakvormige struktuur te vorm. Sy basale wand lê styf teenaan die oorblyfsels van die sinergied in die omgewing van die mikropiel.

Die apikale sel deel dwars, sodat 'n lynvormige, driesellige pro-embrio ontstaan (fig. 3). Die terminale sel (c in fig. 3) ondergaan 'n lengtedeling (fig. 4). Dan volg 'n tweede lengtedeling, reghoekig op die eerste, sodat die boonste sellaaag nou uit vier selle bestaan (fig. 6). Die tweede dogtersel (d in fig. 3) van die apikale sel het intussen dwars gedeel (fig. 5), sodat die pro-embrio nou uit drie gesuperponeerde sellae bestaan (uitgesonderd die basale sel). Die tweede sel (m in fig. 5) deel oorlangs om eers twee, dan vier selle te vorm (fig. 6). Die derde sel (ci in fig. 5) deel ook later oorlangs (fig. 6).

Gedurende selwandvorming in die endosperm is die embrio reeds goedontwikkel en is die protoderm reeds gevorm (fig. 7).

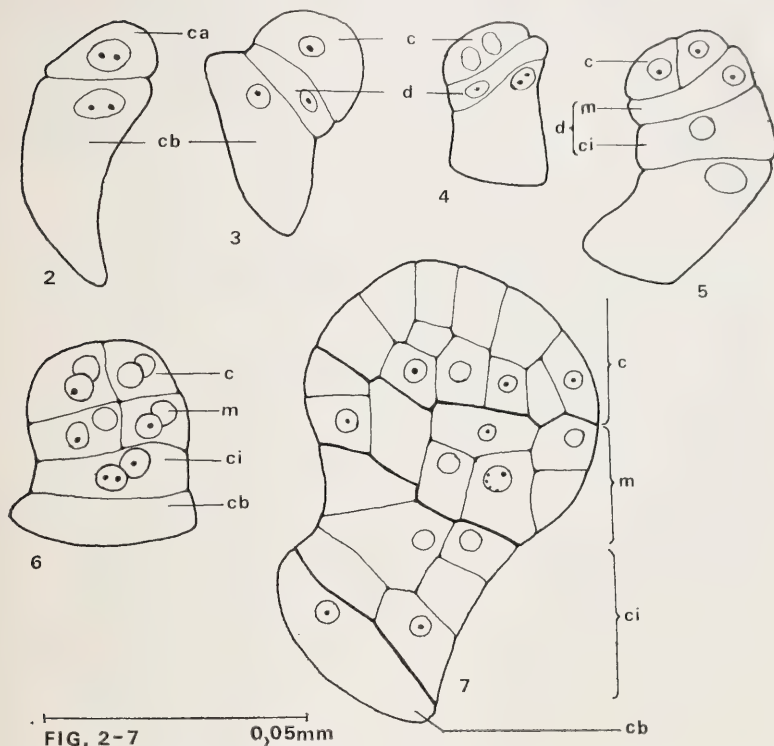
Die embrio-ontwikkeling van *R. rosea* var. *reflexa* stem ooreen met die van die *Sagittaria*-variasie van die Caryophyllaceae-tipe. Volgens Johansen (1950) vorm die boonste sellaaag (c in fig. 6) die saadlob; die tweede sellaaag (m in fig. 6) vorm die boonste deel van die hipokotiel en die stingelgroei punt, terwyl die derivate van die derde sellaaag (ci in fig. 6) die onderste deel van die hipokotiel, die inisiale selle van die wortelkorteks, die wortelmus en die ware suspensor vorm. Die basale sel (cb in fig. 6) het geen aandeel aan die vorming van die ware embrio nie, maar vorm die basale deel van die suspensor en heg die embrio vas aan die embriosakwand.

Ontwikkeling van die saadhuid

Die twee integumente van die saadknop is bedek en geskei van mekaar en van die endospermweefsel deur drie kutikulalae (c_1 , c_2 & c_3 in fig. 8). Die buite-integument is minstens vierlagig, terwyl die binne-integument tweelagig is (fig. 8).

Wanneer die eerste endospermkerne gevorm word, is die buite-epidermis (bu in fig. 8) van die buite-integument groot, reghoekige selle met verdikte buitewande en 'n donkerkleurende inhoud. Die sub-epidermale selle is klein, plat en dunwandig. Die selle van die binne-integument (bui en bi in fig. 8) is groot en reëlmatig.

Wanneer die embriosak gevul is met dunwandige endospermweefsel, word die buite-epidermis van die binne-integument platgedruk en verdwyn, sodat net die kutikulalaag (c_2 in fig. 9) oorbly. Die buite-epidermisselwande van die

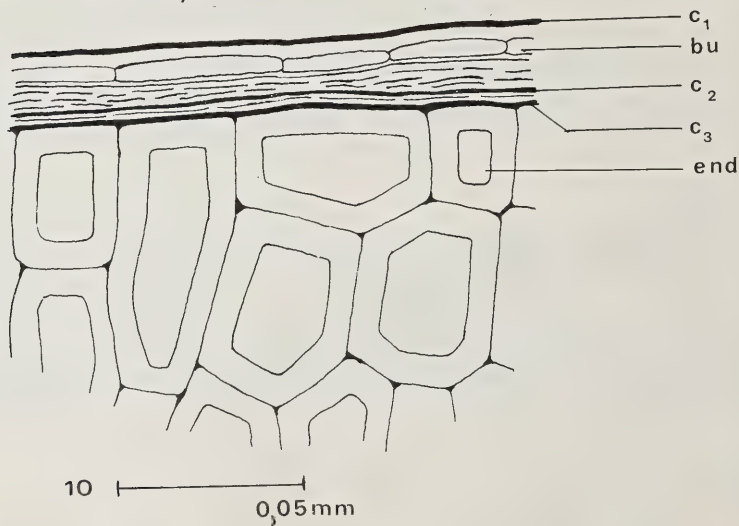
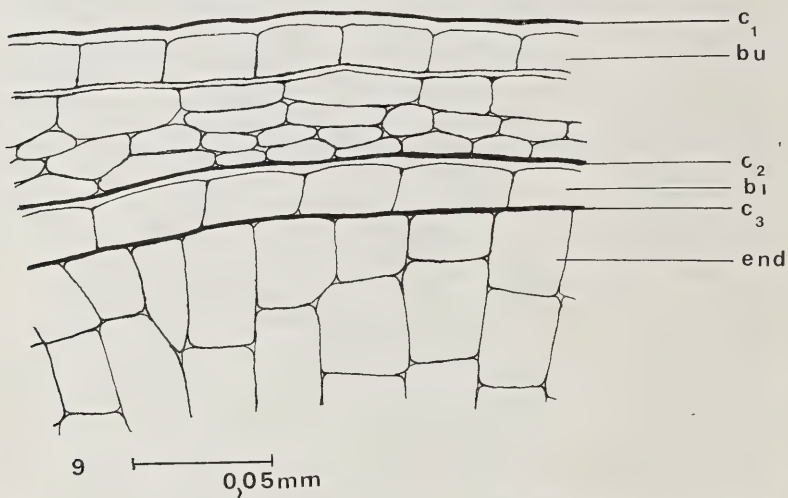
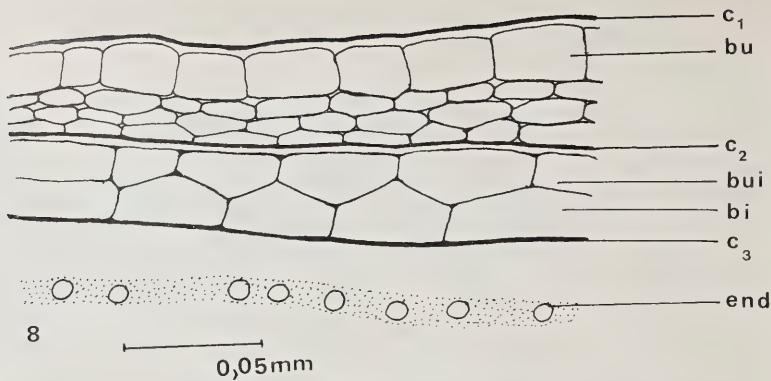


FIGS. 2-7.

Lengtesnee deur die ontwikkelende embrio van *Romulea rosea* var. *reflexa*: 2, dogterselle van die sigoot; 3, liniêre, driesellige pro-embrio; 4, lengtedeling van die apikale sel; 5, pro-embrio bestaande uit vier gesuperponeerde sellae; 6, lengtedelings in die derivate van die apikale sel; 7, embrio waarin protoderm reeds gevorm is; c, boonste dogtersel van apikale sel; ca, apikale sel; cb, basale sel; ci, tweede dogtersel van d; d, tweede dogtersel van apikale sel; m, eerste dogtersel van d.

buite-integument het merkbaar verdik. Die sub-epidermale selle het vergroot en bevat baie setmeelkorrels.

Namate die endospermiswande verdik (fig. 10), verdwyn die inhoud van die selle van die saadhuid. Die buite-epidermisselle (bu in fig. 10) het baie verdikte, gekutiniseerde wande en vorm die vernaamste beskermende laag van die saad. Die oorspronklike kutikulêre lae bly oor tussen die platgedrukte sellae (fig. 10).



BESPREKING

Uit 'n vergelyking van die endosperm-, embryo- en saadhuidontwikkeling van *Romulea rosea* var. *reflexa* en die van die twee Suid-Europese spesies, blyk die volgende verskille:

1. Die embriosak van *R. bulbocodium* (Ferraris, 1902) is heelwat kleiner as die van *R. rosea* var. *reflexa* en die saadknop bevat na bevrugting geen nucellusweefsel nie. By lg. spesies word die chalazale nucellusweefsel eers betreklik laat deur die endospermhaustorium geresorbeer.
2. Geen endospermhaustorium is in die saadknoppe van die Suid-Europese *Romulea*-soorte gevind nie, terwyl die struktuur 'n opvallende kenmerk van die saadknop van *R. rosea* var. *reflexa* is.
3. Volgens Ferraris (1902) word gedurende embryo-ontwikkeling soms vier gesuperponeerde selle deur die verdeling van die apikale sel gevorm, terwyl die basale sel onverdeelde bly. By *R. rosea* var. *reflexa* word, behalwe die basale sel, net drie gesuperponeerde sellae gevorm. Die embryo-ontwikkeling van die twee Suid-Europese *Romulea*-soorte ressorteer dus ook onder die Caryophyllaceae-tipe, maar nie altyd onder die Sagittaria-variasie nie.
4. Die saadhuid-ontwikkeling van *R. rosea* var. *reflexa* en die twee Suid-Europese *Romulea*-spesies is waarskynlik dieselfde. Béguinot het egter die „interne epidermis in kontak met die endosperm” (d.i. die binne-epidermis van die binne-integument) as 'n vername beskermende laag beskou. Hy het waarskynlik net 'n tussen-stadium in die saadhuid-ontwikkeling ondersoek, want sy beskrywing van die saadhuidlae stem ooreen met figuur 9 van die huidige ondersoek. By *R. rosea* var. *reflexa* word hierdie laag later platgedruk en is die buite-epidermis van die buite-integument die vernaamste beskermende laag van die saad.

Soos die verskille in die bou en ontwikkeling van die saadknoppe van die ondersoekte Suid-Europese en Suid-Afrikaanse spesies (Steyn, 1973), is bg. verskille klein. Die embriologie verskaf dus geen bykomende leidrade om die ontwikkelingslyne binne die genus aan te dui nie. Embriologiese eienskappe kan egter van taksonomiese belang wees by die bepaling van groter taksa.

'n Vergelyking van die huidige resultate met bestaande literatuur oor die embriologie van die Iridaceae toon dat *Romulea* embriologies baie ooreenstem met *Crocus* (Haeckel, 1930 en Hofmeister, 1861). Pax (1888) het hierdie twee

FIGS. 8-10.

Langtesneë deur die ontwikkelende saad van *Romulea rosea* var. *reflexa* om saadhuid- en endospermvorming aan te toon: 8, saadhuidlae gedurende vrye endospermkerndeling; 9, saadhuid waarvan die buite-epidermis van die binne-integument verdwyn het en die endosperm dunwandig is; 10, platgedrukte saadhuidlae en dikwandige endosperm; bi, binne-epidermis van binne-integument; bu, buite-epidermis van buite-integument; bui, buite-epidermis van binne-integument; c₁, buitenste kutikulalaag; c₂, middelste kutikulalaag; c₃, binneste kutikulalaag; end, endosperm.

genera onder die Crocoideae geplaas. By beide genera word die nucelluskap voor bevrugting geresorbeer, sodat die sinergiedes wat dieselfde bou vertoon, tot in die mikropielkanaal strek. By die Iridoideae soos *Iris*, *Belamcanda*, *Libertia*, *Aristea* en *Tritonia* word tydens bevrugting nog 'n tweelagige nucelluskap aangetref en die sinergiedes is oor die algemeen kleiner (Haeckel, 1930). Die sekondêre embriosakkern word by beide *Crocus* en *Romulea* net bokant die antipodes aangetref, terwyl dit by *Gladiolus*, *Freesia* en *Ixia* dieper as die antipodes voorkom (Haeckel, 1930).

Die opvallendste en belangrikste embriologiese ooreenkoms tussen *Crocus* en *Romulea* is die bou en posisie van die antipodes. Lg. is groot, omgekeerd peervormige selle wat op 'n chalazale nucellus-pilaartjie gedra word. Hoewel die antipodes by die Ixiodeae ook neig tot hipertrofie, word 'n nucelluspilaartjie nie aangetref nie. Dit ontbreek ook by die Iridoideae waar die antipodes klein bly.

Soos by die Suid-Europese *Romulea*-soorte kom by *Crocus* nie 'n endosperm-haustorium voor nie, maar die endospermweefsel van die ryp saad is dikwandig (Hofmeister, 1861) soos die van *Romulea*. Volgens Netolitzky (1926) bevat hierdie sekondêre verdikte selwande dikwels amyloïed.

'n Belangrike verskil tussen *Crocus* en *Romulea* kom voor in die bou van die volwasse stuifmeelkorrels. Eg. het nie-aperturate of spiraal-aperturate stuifmeel (Erdtman, 1952), terwyl *Romulea* monosulkate stuifmeel het (Erdtman, 1952 en Steyn, ongepubliseerd). Na aanleiding hiervan het Heintze in 1927 (volgens Erdtman, 1952) voorgestel dat *Romulea* vanaf die Crocoideae na die Iridoideae oorgeplaas word. Aangesien die ander embriologiese kenmerke van *Romulea* en *Crocus* so 'n groot mate van ooreenstemming vertoon, kan so 'n oorplasing nie geregverdig word nie.

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CERIOPS TAGAL (PERR.) C. B. ROBINSON AT KOSI BAY

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ABSTRACT

A survey at Kosi Bay revealed that saplings of *Ceriops tagal* (Perr.) C. B. Robinson were common in the estuary, although no living mature trees were found. While prospects for the continued existence of this community are good, there still remains a strong need for protection of this species which has been recorded from no other locality in the Republic of South Africa.

UITTREKSEL

CERIOPS TAGAL (PERR.) C. B. ROBINSON TE KOSIBAAI

'n Opname by Kosibaai het getoon dat jong boompies van *Ceriops tagal* (Perr.) C. B. Robinson algemeen in die estuarium voorkom hoewel geen lewende volgroeide bome gevind kon word nie. Terwyl die vooruitsigte vir die voortbestaan van hierdie gemeenskap goed is, is dit tog nodig dat hierdie spesies, waarvan die voorkoms nêrens elders in die Republiek van Suid-Afrika aangeteken is nie, beskerm moet word.

INTRODUCTION

Previous accounts of the mangroves at Kosi Bay indicated that *C. tagal* was rare (Tinley, 1958; Breen and Hill, 1969). This view would seem to have been confirmed by botanists and wildlife enthusiasts on subsequent visits. In view of the fact that this is the only locality in the Republic of South Africa from which *C. tagal* had been recorded, it was felt that a survey of the current status of this species was essential. This survey was also intended as part of a re-appraisal survey of the mangroves of Natal presently being conducted by Ward.

Consequently two visits were paid to the Kosi Bay lakes, viz. 8-10 October, 1972, and 7-9 December, 1972. The earlier visit was purely a reconnaissance to establish the presence of this species and the approximate numbers and localities. During the second visit distribution and numbers were recorded and measurements made wherever possible.

DISTRIBUTION

The distribution of *C. tagal* in the estuary is shown on the accompanying map (Fig. 1).

As fairly careful observation on the reconnaissance established that this species is absent in the higher reaches of the system, these parts were not included in the survey. The greatest number occurred at A where at least 300 saplings were counted in an area of approximately 0.25ha; in the area of highest

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FIG. 1.
Part of Kosi Estuary showing the distribution of
live *Ceriops tagal*.

concentration a count revealed that there was an average of 65 saplings in an area of 100m². In one spot 37 saplings were counted around two adjacent dead parent trees. These 37 saplings were not included in the above count which would otherwise have been higher.

While there were small local groupings of saplings at other parts of the estuary, nowhere else were they found to be as numerous. In most cases where there was a small colony of saplings there was evidence of the presence of dead mature trees in the immediate vicinity, suggesting that these were the parents of the saplings. The survey also revealed that all the living specimens were saplings up to a height of 1.25m; no mature living trees were seen. The saplings averaged approximately 100 cm in height which indicates that they are all roughly the same age. It is suggested that they became established from propagules released either shortly before, or by dying trees during, the mass mortality of mangroves which occurred in 1965 (Breen and Hill, 1969). There was no evidence of flowering or fruiting in the present community.

CONCLUSIONS

The presence of so many dead parent trees of *C. tagal* indicates that this species was fairly common prior to the mass mortality in 1965. This survey has revealed that, although there appear to be no living mature trees, regeneration of this species in the form of young saplings is good and the prospects for the continued existence of a fairly extensive community at Kosi Bay are encouraging. A disquieting feature is the lack of plants at a reproductive stage. Of interest here are the observations on *Bruguiera gymnorrhiza* (L.) Lam. where plants at heights of 70 cm and 90 cm were found in bud and young fruit respectively. Should the present juvenile *C. tagal* community suffer a recurrence of the 1965 tragedy there will be little prospect of regeneration other than through propagative material floating in from further north. As *C. tagal* has not been found at any other locality in the Republic, it is essential that this southernmost community at Kosi Bay should enjoy the fullest possible protection.

ACKNOWLEDGEMENTS

The writers wish to thank Miss J. Hume for her assistance with the map.

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TWO NEW SPECIES OF *HAWORTHIA* (LILIACEAE)

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ABSTRACT

Two new species of *Haworthia* Duval are described. One of these, *H. serrata* Bayer, is recorded from the Coastal Renosterbos vegetation type southwest of Heidelberg, Cape; and the second, *H. pulchella* Bayer, from the Succulent Karoo southeast of Touws River.

UITTREKSEL

TWEE NUWE *HAWORTHIA* SOORTE (LILIACEAE).

Twee nuwe *Haworthia* (Duval) soorte word beskryf. Een van hierdie, *H. serrata* Bayer is in die Kus Renosterbos veldtipe S. W. van Heidelberg, Kaap en die tweede, *H. pulchella* Bayer in die Sukkulente Karoo S. O. van Touwsrivier gevind.

INTRODUCTION

The recognition, estimation of taxonomic rank, and circumscription of elements in *Haworthia* is problematic. In an already confused taxonomy, the description of new elements is not lightly undertaken. In the present case, *H. serrata* is regarded as an ecologically distinct element in an involved complex south of the Langeberg mountain range of the Southwestern Cape; *H. pulchella* is also a distinctive element with less confusing geographic affinities, occurring in the northwestern area of the Little Karoo.

Haworthia serrata Bayer sp. nov. (Liliaceae—Aloineae) *Foliorum rosula* acaulescens, 4,5–9 cm diam., circa 70 folia. *Caulis* crassus, 1/3 diam. rosula. *Radices* crassae, firmae, albae carnosae, non-fibrosae. *Folia* erecta, expansa, infra recurvae, apices versus incurvati, usque 6 cm longa, 1,2 cm lata, 5 mm crassa, ovata lanceolata acuminata, aristata raro setiferis usque 6 mm longa, ex olivaceus; *supra* plana ad concava ad vases, plana ad convexa versus media et apices, extremum subpellucida nervis 1–4, interdum spinifera tuberculi; *subtus* convexa, carinata ab media, subinde spinifera alba tuberculi, aequae ex olivaceus; *marginis* acutae, carinata et marginis spinis; *spinae* translucentes albae, 1–2 mm longae, 2–3 mm distans, rectae vel leviter retrorsae.

Pedunculus simplex, 1,6–3 mm diam., circa 45 cm longus racemo incluso, fuscus-viridis; *basis* albae, 3–5 angulatae; *racemus* usque 20 cm longus, flores 20–40, 2–6 apertus; *pedicelli* 1–1,5 mm longi; *bracteae steriles* 8–16, usque 15 mm longae, caudatae; *bracteae fertiles* 8–11 mm longae, auriculatae.

Perianthium album, 14–15 mm longum; *gemmae* leviter biarcuatae. *Florescentia* Sept.–Oct.

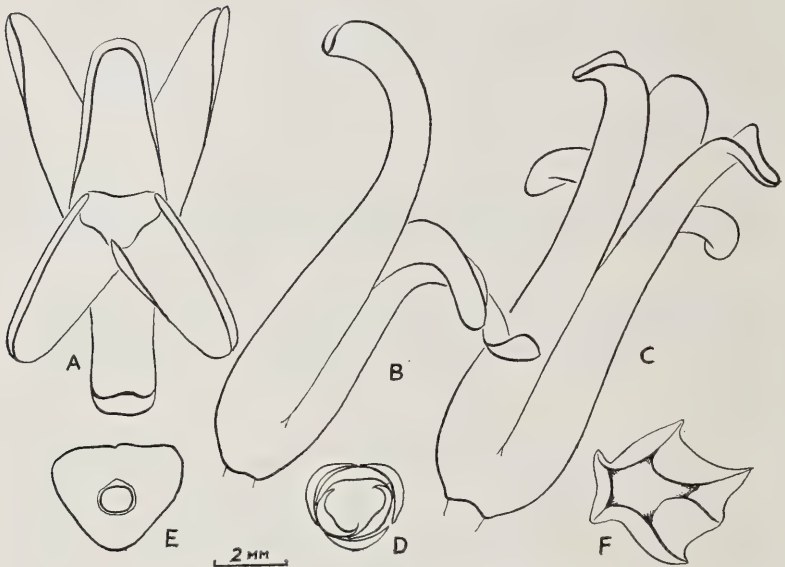


FIG. 1.
H. serrata Bayer sp. nov. Diagram of flower.

Rosette acaulescent, 4,5–9 cm diam., up to 70 leaves. *Stem* thick, up to 1/3 diam. of rosette, not elongate, seldom proliferous. *Roots* thick, firm, white fleshed. *Leaves* erect, spreading, recurved below, incurved at tips, up to 6 cm long, 1,2 cm broad, 5 mm thick, ovate lanceolate acuminate, aristate with rarely setiferous bristle up to 6 mm long, light olive-green; *face* flat to concave at base, flat to convex towards middle and tip; subpellucid end-area with 1–4 veins, 1 generally prominent and reaching tip, occasional spiny excrescences; *back* convex, keeled from middle, uniformly light olive-green with occasional white spined or spineless excrescences; *margins* acute, keel and margins with spines; *spines* translucent white, 1–2 mm long, 2–3 mm apart, straight or slightly retrorse. *Peduncle* simple, 1,6–3 mm diam., up to 45 cm long including raceme, brownish green; *base* white, 3–5 angled; *raceme* up to 20 cm long, 20–40 flowers, 2–6 flowers open; *pedicels* 1–1,5 mm long; *sterile bracts* 8–16, up to 15 mm long, often markedly caudate; *fertile bracts* 8–11 mm long, up to 8 mm wide, auriculate. *Perianth* white, veins broadly greenish brown, 14–15 mm long, upper outer segments erect, plicate at tips with outer margins incurved, inner lower segments with upper margins incurved to tips, tube green inside; *buds* slightly biarcuate, tips lightly flattened dorso-ventrally. Flowering Sept.–Oct.

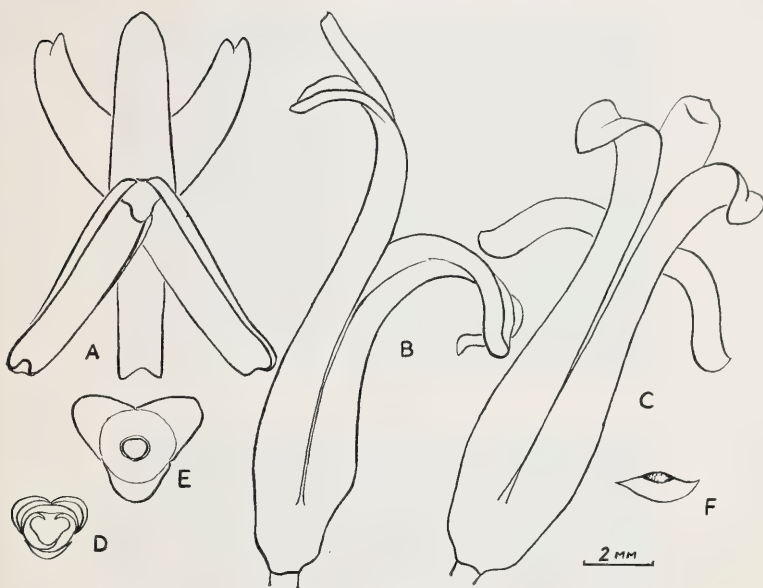


FIG. 2.

H. pulchella Bayer sp. nov. Diagram of flower. (a) flower face, (b) profile, (c) top view, (d) cross section, (e) view of perigon, (f) view of peduncle base.

Type: CAPE-3420 (Bredasdorp): Oudekraalkop, 40 km S.W. of Heidelberg, (BA), Bayer KG 318/71 (holotype NBG.)

H. serrata resembles *H. triebneriana* V. Poelln. (Springfontein, Ladismith, Bayer KG 163/71), but is more opaque, larger and less turgid, the marginal spines are considerably bigger, and the leaves less maculate. This species also has the nearly sessile flowers, broad flower bracts and green colouration, but the flattened bud tip is more a characteristic of the main body of similar budded species in the southwestern Cape. Here *H. serrata* is nearest to *H. heidelbergensis* Smith, ex type locality, and allied populations at Matjestoon, 32 km s.w. of Heidelberg, *H. rossouwii* V. Poelln. from 19 km n. of Bredasdorp and *H. sublimpidula* V. Poelln. near Drew, Swellendam. These are all smaller species with narrower flowers (3 mm at widest), in which the outer tepals are separated along the margins, the marginal spines are considerably smaller and flowering times are different. Despite the restricted locality, *H. serrata* is a distinct element in the complex south of the Langeberg mountain range. This species is so named on account of the regular prominently setate saw-like leaf margins. The writer



FIG. 3.



FIG. 4.

FIGS. 3-4.

H. serrata Bayer sp. nov. KG 318/71, Oudekraalkop, Heidelberg, Cape.

was directed to the plants in the field by Mr. and Mrs. J. N. O. Uys, owners of the farm Oudekraalkop.

Haworthia pulchella Bayer sp. nov. (Liliaceae-Aloineae) *Foliorum* rosula acaulescens, 1,5-4,5 cm diam., circa 45 folia. *Caulis* 5 mm diam., 1/6 diam. rosula. *Radices* usque 2,5 mm diam., luteolae ad bruneolae carnosae. *Folia* erecta, apices versus incurvati, usque 27 mm longa, 7, lata, 1,5 mm crassa, subovata lanceolata acuminata, aristata 1 mm longa, atroviridia; *supra* leviter concava ad bases; *subtus* convexa, valde carinata ab prope bases; *marginis* acute; *spinæ* translucens albae, usque 1,2 mm longae, 1-2 mm apart. *Pedunculus* simplex 0,75-1 mm diam., 30-35 cm longus racemo incluso, subroseus-



FIG. 5.



FIG. 6.

FIGS. 5-6.

H. pulchella Bayer sp. nov. KG 43/71, Avondrust, Touws River.

fuscus; *basis* 2 angulatae; *racemus* 8-10 cm longus, flores 5-12, 1-2 apertus; *pedicelli* 0,5 mm diam., 3-5 mm longi; *bracteae steriles* 7-11, 4-6 mm longae; *bracteae fertiles* 3-5 mm longae. *Perianthium* album, 14-15 mm longum.; *gemmae* angustatae elongatae, fere acuta. *Florescentia* Dec.

Type: CAPE-3320 (Montagu): Avondrust, S.E. of Touws River, (-AC), Bayer KG 43/71, holotype NBG.

Rosette acaulescent, 1,5-4,5 cm diam., up to 45 leaves. *Stem* thin, up to 5 mm diam., about 1/6 diam. of rosette, not elongate, seldom proliferous. *Roots*

thin, up to 2.5 mm diam., yellowish to light-brown flesh, non-fibrous. *Leaves* incurved, erect, firm, up to 27 mm long, 7 mm broad, 1.5 mm thick, subovate lanceolate acuminate, shortly aristate with bristle up to 1 mm long, dark green above, whitish below, surface minutely granulate, marked with longitudinal lines and a few transverse veins; *face* slightly convex at base, 3–4 longitudinal lines; *back* convex, 4–6 faint longitudinal lines, strongly keeled from base, from near middle when turgid, keel with up to 8 reflexed spines usually in 1 but occasionally in 2 parallel rows; *margins* acute, spined in upper half, occasionally from 1/3; *spines* translucent white, up to 1.2 mm long, 1–2 mm apart. *Peduncle* simple, 0.75–1 mm diam., 30–35 cm long including raceme, pinkish-brown; *base* 2-angled; *raceme* 8–10 cm long, 5–12 flowers, 1–2 open; *pedicels* 0.5 mm diam., 3–5 mm long; *sterile bracts* 7–11, 4–6 mm long; *fertile bracts* 3–5 mm long. *Perianth* white, thin brownish nerves, 14–15 mm long, upper outer segments suberect, very lightly plicate at tips, inner lower segments with upper margins strongly incurved proximally, tube very pale green; *buds* narrow elongate, arcuate, younger buds rounded at tips. *Flowering* Dec.

The affinities of *H. pulchella* are uncertain. Vegetatively, the nearest relative may be *H. monticola* Fourcade from the Molen River–Herold area which, however, has the long narrow leaves of the section *Loratae* S.D. The rather narrow elongate buds and tepals are also indicative of affinity with *H. monticola*. The compact growth form is characteristic of *H. marumiana* Uitew. and is also found in *H. herbacea* (Mill.) Stearn and some forms of *H. schuldiana* V. Poelln. *H. pulchella* is quite at variance with these species as far as nuances of leaf colour, marking and texture are concerned. Of particular note is that this species is geographically well separated from possible allies although it does grow in close proximity to *H. setata* Haw. *H. pulchella* is found in the area extending from Avondrust to Nougaspoort, southeast of Touws River. It was first recorded from Avondrust by the late Mr R. C. Littlewood and recollected by Mr F. J. Stayner and the writer.

ROOT AND CROWN ROT OF SILVER TREES*

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ABSTRACT

Greenhouse and field inoculations showed *Phytophthora cinnamomi* Rands to be the primary cause of root and crown rot, and subsequent dieback of the silver tree, *Leucadendron argenteum*. Other related hosts were also recorded, though certain *Protea* spp. appear to be tolerant to the disease.

UITTREKSEL

WORTEL EN KRAAGVERROTING BY SILWERBOME

Inokulasies in die glashuis en in natuurlike omgewings het getoon dat *Phytophthora cinnamomi* Rands primêr verantwoordelik is vir die wortel- en kraagverrotting en die gevolglike afsterwing van silwerbome, *Leucadendron argenteum*. Verwante gashere is ook aangetoon, alhoewel sekere *Protea* spp. verdraagsaamheid teen die siekte openbaar het.

INTRODUCTION

Silver trees (*Leucadendron argenteum*) are subject to a sudden dieback which is of common occurrence throughout the Western Cape. The first indication of disease is the wilting of the entire tree, but removal of the external bark of recently killed trees exposes a dark patch of rotted bark extending from the crown into the root (Fig. 1). This browning may also occur on some apparently healthy trees but is masked by the external bark.

Olivier (1951) and Wager (1970) ascribed dieback of silver trees to infection by the fungus *Botryosphaeria ribis* (Tode ex Fries) Gross & Dugg. However, Olivier's (1951) work was inconclusive in that inoculations of fully grown silver trees with *B. ribis* consistently failed to induce the disease.

The present investigation was carried out to establish the primary cause of dieback of silver trees.

MATERIAL AND METHODS

Isolation

Naturally infected plant material from Stellenbosch, Banhoek, Paarl, Somerset West and Kirstenbosch was plated out on corn meal agar after surface

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* Results to be submitted in partial fulfilment for a Ph.D. degree at the University of Stellenbosch.



FIG. 1.
Rotted bark of the crown of a silver
tree after removal of the external bark.



FIG. 2.
Lesions around cracks in the trunk of
a silver tree from which *Botryosphaeria*
ribis was isolated. External bark re-
moved.



FIG. 3.
Lesion, causing shoot dieback of silver
tree, from which *Botryosphaeria ribis*
was isolated. External bark removed.



FIG. 4.
Wilting of a two-year-old silver tree
after inoculation with *Phytophthora*
cinnamomi. Control plant on the left.

disinfection for one minute with 2% sodium hypochlorite. Fungus isolates were subcultured and stored on potato-dextrose agar (PDA).

Inoculations

Inoculation was by means of the cork-borer method of Sewell and Wilson (1959). Agar discs were cut from well developed colonies of the test organism on PDA, while uninoculated PDA discs were used as control inoculum. Inoculation sites were sealed with vaseline. Except in the case of older trees, where inoculations were as high as four feet above soil surface, all inoculations were made near or at soil level.

Both potted plants in the greenhouse and plants in their natural environment at Kirstenbosch were inoculated. In greenhouse tests 27 silver trees, approximately two years old, were inoculated with *Phytophthora cinnamomi*, *B. ribis* and control inoculum. Three plants in each inoculation group were then held under each of the following temperature regimes: low (13–16C), high (24–31C) and fluctuating (10–25C). The experiment under the high temperature range was duplicated. Silver trees inoculated in their natural habitat were approximately two years old (four trees), six years old (four trees) and more than ten years old (one tree, four groups of inoculations). *Leucospermum cordifolium* (Salisb.) ex Knight Fourcade (one plant, two groups of inoculations) and *L. glabrum* Phillips (one plant, two groups of inoculations) were about five years old and were inoculated with *P. cinnamomi* only.

RESULTS

Isolations from naturally infected plants

Isolations from naturally infected silver trees yielded two fungi; one was constantly isolated from freshly rotted tissues of the crown. It was identified as a *Phytophthora* sp. and specifically as *P. cinnamomi* after comparison with an isolate from grapevine (Van der Merwe & Matthee, 1972) identified by the Commonwealth Mycological Institute. The other fungus was isolated from lesions around cracks (Fig. 2) and from shoots showing dieback (Fig. 3). It was also occasionally associated with *P. cinnamomi* in rotted crown tissues, especially in advanced stages of decay. It was a pycnidial fungus corresponding with the *Dothiorella* stage of *B. ribis*. Although no ascigerous stage developed, it was identified as the imperfect stage of *B. ribis* (personal communication, W.F.O. Marasas, Plant Protection Research Institute, Pretoria). The behaviour of the fungus in culture was also similar to that of *B. ribis* as described by Olivier (1951).

In addition to silver trees, *P. cinnamomi* was isolated from the following Proteaceae showing dieback symptoms: *Leucadendron tinctum* Williams, *Leucospermum lineare* R. Br., *L. cordifolium* and *L. reflexum* Buck ex Meisn.



FIG. 5.

Lesion development on a young potted silver tree three months after inoculation with *Botryosphaeria ribis*. External bark removed.



FIG. 6.

Lesion development following inoculation of a young silver tree with *Phytophthora cinnamomi*. External bark removed.



FIG. 7.

Lesions on a full grown silver tree 10 days after inoculation with *Phytophthora cinnamomi*. Control inoculation in the centre. External bark removed.

Inoculations

Greenhouse inoculations

All plants inoculated with *P. cinnamomi* developed brown lesions similar to those observed in naturally-infected trees. Plants at low and fluctuating temperatures developed the brown discolouration only at the inoculation sites but none died within a period of three months after inoculation. In contrast, all plants held at high temperatures died within 10–12 days (Fig. 4).

Inoculations with *B. ribis* were also positive, though the browning was limited (Fig. 5) and contrasted markedly with the progressive browning (Fig. 6) caused by *P. cinnamomi*. None of the plants inoculated with *B. ribis* died within the observation period of three months.

Inoculations of plants in their natural habitat

All trees growing in their natural habitat and inoculated with *P. cinnamomi* developed typical browning around the point of inoculation (Fig. 7). This was usually followed by rapid wilting of the tree. The younger trees died within ten days of inoculation, while older trees survived for longer periods. After 12–15 weeks only the oldest tree, which died two months later, remained alive.

Inoculation of silver trees with *B. ribis* was also successful, although limited lesion development began only 12–15 weeks after inoculation. No trees died within this period.

Both the *Leucospermum cordifolium* and *L. glabrum* plants died within ten weeks of inoculation with *P. cinnamomi*, the symptoms being typical of those on naturally-infected plants.

Re-isolation

Both *P. cinnamomi* and *B. ribis* were consistently re-isolated from lesions developing after inoculation with the respective organism.

Occurrence of *P. cinnamomi* on *Proteaceae*

Phytophthora cinnamomi was isolated from the crown and root tissues of recently-killed plants of the following species growing in their natural habitat or under cultivation.

Leucadendron argenteum

L. tinctum

L. salicifolium

Leucospermum cordifolium

L. reflexum

L. lineare

L. catherinae

Preliminary investigations indicate that certain *Proteas* pp., (eg *P. cynaroides*), are tolerant to this disease.

DISCUSSION

Phytophthora cinnamomi has an extremely wide host range which includes many Proteaceae (Zentmeyer & Thorn, 1967; Robertson, 1969; Weste & Taylor, 1971; Davison, 1972; Podger, 1972; Newhook & Podger, 1972). The present investigation has shown that it also causes a sudden dieback of silver trees, and that the dieback occurs at high temperatures. The effect of high temperatures in enhancing disease development was also noted in Australia where *P. cinnamomi* is particularly destructive to local Proteaceae during the spring and summer months (Newhook & Podger, 1972). It is therefore postulated that *P. cinnamomi* is the pathogen responsible for the common dieback of silver trees and certain other Proteaceae in South Africa.

Botryosphaeria ribis, although a major pathogen, is not regarded as a primary cause of dieback of silver trees.

Although the full host range of *P. cinnamomi* among South African Proteaceae has not been determined, it appears that certain *Protea* spp., notably *P. cynaroides*, are tolerant to the disease. The nature of this resistance is at present under investigation.

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AN EVALUATION OF TECHNIQUES USED FOR EXTRACTING ENDOGENOUS CYTOKININS FROM PLANT MATERIAL

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(Department of Botany, University of Natal, Pietermaritzburg)

ABSTRACT

Using paper and column chromatography it was found that considerable amounts of cytokinins can be lost from aqueous plant extracts during purification by solvent partitioning. Most, if not all, of the free base cytokinins present in seed extracts of *Rumex obtusifolius* partitioned into petroleum ether at pH 9.0 and ethyl acetate at pH 2.5. Whether the presence of these compounds will be detected by paper chromatography depends very much on the solvent system used.

UITTREKSEL

'N EVALUASIE VAN TEGNIEKE OM SITOKINIENE UIT PLANTMATERIAAL TE EKSTRAHEER.

Met behulp van papier- en kolomchromatografie is gevind dat wanneer plantekstrakte met behulp van organiese oplosmiddels gesuiwer word, relatief groot hoeveelhede van die sitokiniene verlore gaan. Die meeste van die vrye basis sitokiniene in saadekstrakte van *Rumex obtusifolius* beweeg byvoorbeeld in petroleumeter, pH 9,0, en etielasetaat, pH 2,5, in. Of die teenwoordigheid van sodanige verbindings met behulp van papierchromatografie aangetoon sal word, hang grotendeels af van die chromatografiese oplosmiddels wat gebruik word.

INTRODUCTION

The endogenous cytokinins extracted from plant material with aqueous methanol or ethanol are usually purified to some degree prior to being bio-assayed. This is frequently done by partitioning the extracted substances with one or more organic solvents at different pH values.

Pigments and fatty substances have been removed from aqueous plant extracts, at pH 9.0, by partitioning with petroleum ether (Gazit and Blumenfeld, 1970; Prakash and Maheshwari, 1970). These authors could detect no cytokinin activity in the petroleum ether fraction. However, Van Staden and Wareing (1972) have reported cytokinin activity in such extracts. As a number of synthetic cytokinins did not partition into petroleum ether at pH 9.0 it was, at the time, suggested that the activity was perhaps due to substances that are less polar than the substituted adenines which constitute the known cytokinins. This however, does not mean that the natural cytokinins would behave similarly.

In order to remove acidic inhibitors, gibberellins and auxins from plant extracts the pH values of these extracts are adjusted to 2.5 before partitioning against ethyl acetate. That no cytokinin activity could be detected in the ethyl acetate fraction (Gazit and Blumenfeld, 1970; Mayak and Halevy, 1970; Van Staden and Wareing, 1972) is perhaps not surprising as they will contain phenolic compounds as well as inhibitors that would have an adverse effect in most

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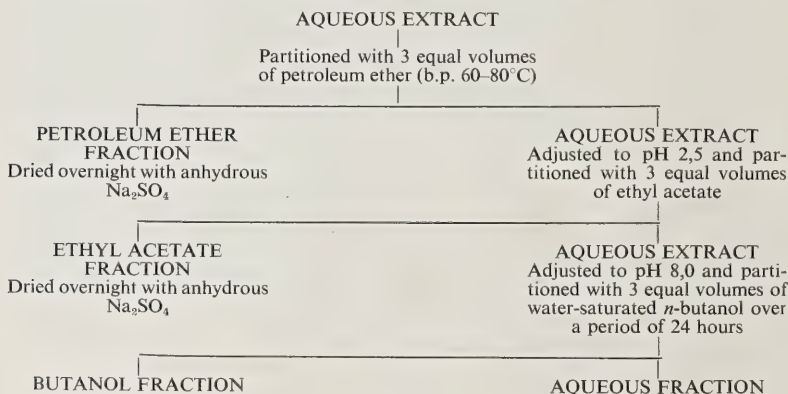
bioassays. In many laboratories ethyl acetate is used routinely for the extraction of cytokinins from aqueous extracts at high pH values; 8,2–8,6 (Upper, Helgeson, Kemp and Schmidt, 1970; Phillips and Cleland, 1972). Thus it is quite possible that even at lower pH values considerable quantities of cytokinin could move into ethyl acetate, but their activity would be masked by interfering compounds.

Following the above partitionings the cytokinins are frequently separated into the butanol-soluble free bases and nucleosides, and the water-soluble nucleotides by partitioning against water-saturated *n*-butanol. It is significant that considerable amounts of butanol-soluble cytokinins may remain in the aqueous extract (Tegley, Witham and Krasnuk, 1971). Their presence could be the result of incomplete partitioning or breakdown of the remaining nucleotides.

The present investigation was an attempt to establish to what extent cytokinins are lost during solvent partitioning, and whether the masking effect of impurities can be eliminated by using different chromatographic solvent systems. Although the soybean callus assay is probably one of the most specific and reliable (Letham, 1967), different results might be obtained when other bioassays are used.

MATERIAL AND METHODS

Ten gram samples of seed of *Rumex obtusifolius* L. were incubated at 20°C on moist filter paper in the dark for 48 hours. They were then exposed to 15 minutes red light and incubated for a further two days in the dark. At the end of this period the seed was ground in 500 ml 80% ethanol and extracted for 24 hours at 4°C and then filtered. The residue was washed with a further 250 ml ethanol and then discarded. The combined filtrates were reduced to the aqueous phase, brought to 100 ml, adjusted to pH 9,0 and extracted as follows:



Only redistilled solvents were used for partitioning. All fractions were taken to dryness under vacuum at 35°C, redissolved in 80% ethanol and streaked on Whatman No. 3MM chromatography paper and developed with solvent system A, viz., water-saturated *sec*-butanol. In addition, the following solvent systems were employed: B, *sec*-butanol: 25% ammonium hydroxide (4:1 v/v); C, *iso*-propanol: ammonia: water (10:1:1 v/v). Each chromatogram was thoroughly air dried and divided into 10 equal Rf strips. Each strip was assayed separately for cytokinin activity using the soybean callus bioassay. The different fractions were also fractionated on a Sephadex LH-20 column (2,5 × 90 cm) as described by Armstrong, Burrows, Evans and Skoog (1969). The cytokinins were eluted with 35% redistilled ethanol at a flow rate of 20 ml/hour. Forty millilitre fractions were evaporated to dryness at 30°C and assayed for cytokinin activity. Three callus explants were transferred to each flask and maintained at $25 \pm 3^\circ\text{C}$ under continuous illumination for 28 days. The values presented in the figures are the means of the separate extractions and bioassays.

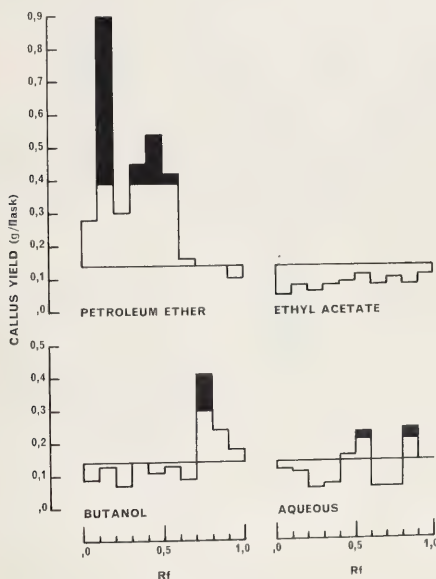


FIG. 1.

Histograms of soybean callus bioassays of extracts from ten grams dry weight equivalent of *Rumex* seed after paper chromatography in water-saturated *sec*-butanol. The black areas represents activity statistically significant from controls at the one per cent level.

RESULTS AND DISCUSSION

When the plant extracts obtained from *Rumex* seed were separated in solvent system A most cytokinin activity was evident in the petroleum ether fraction (Fig. 1). This, however, may not be a true reflection, as the petroleum ether fraction is relatively "clean" compared with the ethyl acetate, butanol and aqueous fractions which contained large amounts of phenolics and other impurities. Furthermore, these impurities have the tendency to streak over most of the chromatogram when water-saturated *sec*-butanol is used. It is thus quite possible that the cytokinin levels in the ethyl acetate, butanol and aqueous fractions are higher than indicated by the bioassays (Fig. 1). That this is actually the case was shown, when most of the impurities were eliminated by using other chromatographic solvent systems. When solvent systems B and C were used it became apparent that the butanol fraction contained a higher concentration of cytokinin than the petroleum ether fraction (Figs. 2 and 3). This was further substantiated when the extracts were fractionated on a Sephadex LH-20 column (Fig. 4). Elimination of interfering substances also revealed that rela-

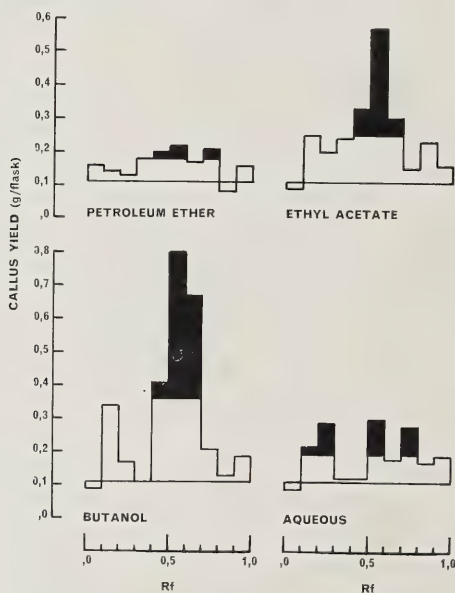


FIG. 2.

Histograms of soybean callus bioassays of extracts from ten grams dry weight equivalent of *Rumex* seed after paper chromatography in *sec*-butanol: 25% ammonium hydroxide (4:1 v/v). The black areas represents activity statistically significant from controls at the one per cent level.

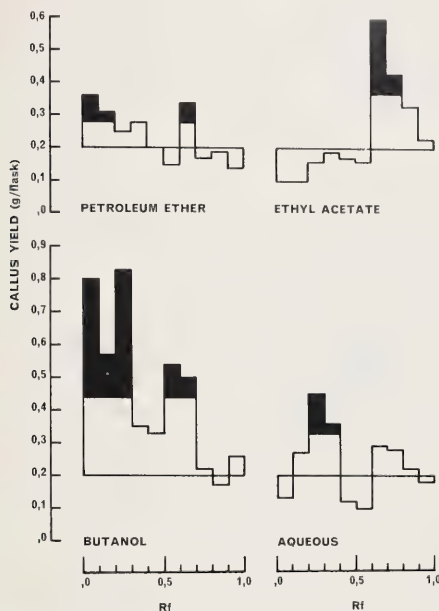


FIG. 3.

Histograms of soybean callus bioassays of extracts from ten grams dry weight equivalent of *Rumex* seed after paper chromatography in *iso*-propanol: ammonia: water (10:1:1 v/v). The black areas represents activity statistically significant from controls at the one per cent level.

tively large amounts of cytokinin were present in the acidic ethyl acetate fraction, which showed no signs of activity when separated with solvent A. These results clearly demonstrate that failure to detect cytokinin activity may be due to incomplete removal of interfering substances.

By fractionating plant extracts on a Sephadex LH-20 column Armstrong *et al.* (1969) were able to separate free base and nucleoside cytokinins. The present results obtained with paper chromatography indicate that cytokinins can partition into all of the solvents used. However, as the free bases and nucleosides do not separate clearly from one another in the solvent systems, no information is available as to the possible nature of the cytokinins involved. The different fractions were therefore separated by column chromatography. This yields more information about the nature of the compounds and excludes the toxic effect of residual alcohols and/or ammonia from the solvent systems in the bioassay. The results in Figure 4 also demonstrate that cytokinins were present in all fractions. Of particular significance is the fact that the major

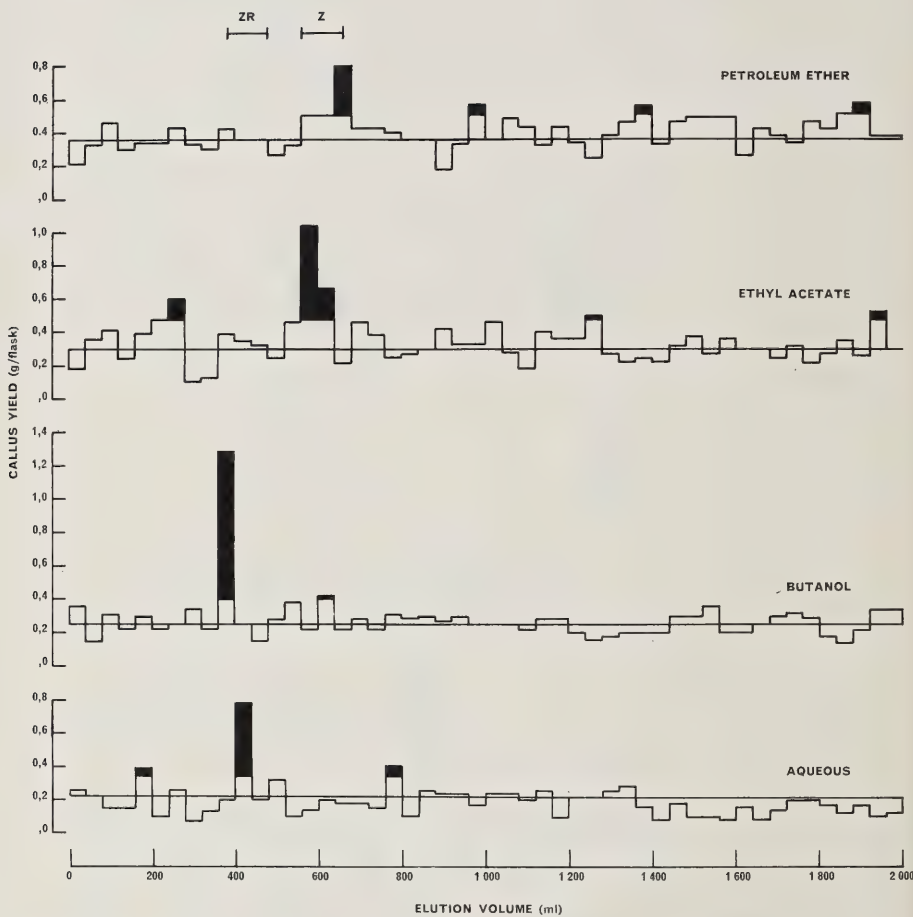


FIG. 4.

The distribution of cytokinin activity of a Sephadex LH-20 fractionation of extracts from ten grams dry weight equivalent of *Rumex* seed. The column was eluted with 35% ethanol at a flow rate of 20 ml/hour. The black areas represents activity statistically significant from controls at the one per cent level. Z = zeatin, ZR = zeatin riboside.

peak of activity in the petroleum ether and ethyl acetate fractions co-chromatographed with zeatin. Whilst it is appreciated that this cannot be regarded as proof of identity it suggests that free bases will readily partition into these solvents. The major peak of cytokinin activity in the butanol and aqueous fractions co-chromatographed with zeatin riboside. Very little activity was found in these fractions in that region where zeatin normally elutes. The presence of cytokinin activity in the aqueous fraction that co-chromatographed with zeatin riboside could result from incomplete partitioning against butanol, even after 24 hours. Alternatively the nucleotide could have been hydrolyzed to its corresponding nucleoside.

From the data presented it is evident that considerable amounts of cytokinin can be lost during purification by partitioning. In fact most of the free base cytokinins in the seed extracts appeared to have been lost by partitioning against petroleum ether and ethyl acetate (Fig. 4). If these fractions are not properly screened for cytokinin activity one could easily be led to believe that only nucleosides were present in the plant extracts. If the plant extracts under investigation are reasonably pure it would probably be advisable to eliminate solvent partitioning to an absolute minimum.

When the primary object of the investigation is to identify endogenous cytokinins these losses are probably not serious although inconclusive results would be obtained if the cytokinin concentration is low. However, in studies where the possible participation of endogenous cytokinins in physiological phenomena is investigated the losses are significant.

ACKNOWLEDGEMENTS

This research was supported by a grant from the Council for Scientific and Industrial Research, Pretoria, Republic of South Africa.

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NEW COMBINATIONS IN XEROPHYTA JUSS. (VELLOZIA VAND. PRO PARTE)

H. COETZEE and H. P. VAN DER SCHIJFF

(*Department of General Botany, University of Pretoria.*)

A morphological taxonomical study of the species of Velloziaceae in South Africa and South West Africa was undertaken and the following new combinations are proposed:

Xerophyta retinervis Bak. var. **equisetoides** (Bak.) Coetzee stat. nov.

X. equisetoides Bak. in J. Bot. Lond. **13**:233 (1875). Type: Rhodesia, South African Goldfields, *Baines* (K, holo. PRE, photo).

Vellozia suaveolens S. Greves in J. Bot. Lond. **59**:282 (1921) Syntypes: Rhodesia, Bernheim Hill, Mazoe, *Monro* 2174, *Eyles* 439 (BM).

var. **wentzeliana** (Harms) Coetzee stat. nov. *Barbacenia wentzeliana* Harms in Bot. Jahrb. **30**:277 (1902). Type: East Africa, Tanzania, Unyika, Sante village on the Yamba River, *Goetze* 1409 (B).

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A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION, CONCLUSION, ACKNOWLEDGMENTS, etc.

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arranged chronologically by basionyms. Whenever possible, the types of the basionyms should be cited, e.g.:

Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. **1960**: 307 (1960).

Chrysophyllum magalismontanum Sond. in Linnaea **23**: 72 (1850). Type: Magaliesberg, Zeyher, 1849 (S, holo.; BOLI, SAM!).

Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

Pouteria magalismontana (Sond.) A. Meeuse in Bothalia **7**: 335 (1960).

Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. **3**: 641 (1898). Syntypes: Angola, Welwitsch 4827, 4828, 4829 (BM!).

Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal Wilms 1812 (B†, holo.; K!).

Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

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REFERENCES

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Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy*. Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia*. *Jl S. Afr. Bot.* **26**: 139-148.

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THE USE OF THE NAME *LEUCADENDRON AUREUM* BURM. f.

J. P. ROURKE

(Compton Herbarium, Kirstenbosch)

ABSTRACT

As *Leucadendron aureum* Burm f. is based on two discordant elements, it is suggested that this name be rejected.

UITTREKSEL

DIE GEBRUIK VAN DIE NAAM *LEUCADENDRON AUREUM* BURM. f.

Leucadendron aureum Burm. f. is op twee onverenigbare elemente gebaseer. Dit word voorgestel dat die naam verwerp word.

INTRODUCTION

In a number of local herbaria, a tentative name change for *Protea longiflora* Lam. was suggested on determinavit labels attached to specimens of this species. Such a name change would have involved the making of a new combination—a combination which has never actually been published. Unfortunately, the name which would have resulted from the combination, *Protea aurea*, was assumed to have been published in some quarters and has already been used in scientific literature in at least one paper known to the writer. (Schutte, K. H., 1973. Comparative transpiration studies in some Cape Proteas. *S. Afr. J. Sci.* 69: 57-58). As no basionym was cited and no description provided, the name *Protea aurea* must rank as a *nomen nudum*. It is important that the usage of the *nomen nudum*, *Protea aurea*, be discontinued forthwith: *Leucadendron aureum* Burm. f., which might have been used as the basionym for the combination, must be rejected under Article 70 of the International Code of Botanical Nomenclature, as it is based on two entirely discordant elements. The rejection of the name *Leucadendron aureum* Burm. f. is discussed below.

REJECTION OF *LEUCADENDRON AUREUM* BURM. f.

When N. L. Burman published the binomial *Leucadendron aureum* Burm. f., no description was given but he did cite a plate and description in Herman Boerhaave's *Index Alter Plantarum*: 199, t. 199 (1720). The engraving (fig. 1.) in this publication shows a flowering branch of *Protea longiflora* Lam., with a bud and an open inflorescence (labelled F), below which is a ripe dehiscing female cone of *Leucadendron pubescens* R. Br. (labelled G). The two fruits (L) and perianth (M) next to the cone are also quite clearly those of *Leucadendron pubescens* R. Br. In his description, Boerhaave states that the cone (*Leucadendron pubescens*) arises in the middle of the inflorescence (*Protea longiflora*) on the

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CONOCARPODENDRON; folio subrotundo, crasso, rigido, valde nervoso; cono longo variegato ex rubro & lavo; flore aureo.

Fig. 1. Plate 199 in Boerhaave's *Index Alter Plantarum* which serves as the type of *Leucadendron aureum* Burm. f.

flowering shoot. This may be seen from the relevant portion of Boerhaave's highly fanciful description, which, translated from the Latin reads:—

“Thereupon an opening in the flower (F) is established so that in the middle it becomes a scaly cone (G) . . .”

Boerhaave concludes with a more detailed description of the cone and fruits (*Leucadendron pubescens*), which he again asserts are the fruits of the inflorescence (*Protea longiflora*). It is not surprising that Boerhaave conjured up so whimsical a description, for it must be remembered that his information was based entirely on illustrations prepared at the Cape and loaned to him by Hartog. These Boerhaave subsequently copied and reproduced in the *Index Alter Plantarum* (van Oostroom, 1951). There is not a shred of evidence to indicate that Boerhaave ever saw dried specimens of the 24 Cape Proteaceae which he described in this work. Evidently, he accepted each of Hartog's plates as representing a single taxon which explains his curious account of the specimens figured on plate 199.

It should be noted that the anomalies in Boerhaave's plate 199 in the above-mentioned work have been commented on by previous authors (Brown, 1810: 76; Williams, 1972: 5), but no attempt has yet been made to suppress the name, *Leucadendron aureum* Burm. f., based on this plate.

CONCLUSION

It is evident that *Leucadendron aureum* Burm. f. is based on two entirely discordant elements and since, in the absence of a description by Burman, it is impossible to select one of the two elements as a satisfactory type, the name must therefore be rejected under Article 70 of the International Code of Botanical Nomenclature. *Protea longiflora* Lam. thus remains the earliest available epithet to be applied to this species.

SYNONYMY

Protea longiflora Lam., Tabl. Encycl. **1**: 234 (1792); R. Br. in Trans. Linn. Soc. Lond. **10**: 76 (1810); Hook. in Curtis's Bot. Mag. **54** t. 2720 (1827); Meisn. in DC., Prodr. **14**: 234 (1856); Phill. & Stapf in Fl. Cap. **5**: 577 (1912). Type: Cape of Good Hope, without collector, in herb Lamarck (P—LA!).

Leucadendron aureum Burm. f., Prodr. Fl. Cap.: 4 (1768)—nom. rej. Type: Boerhaave, Ind. Alt. Plant. t. 199 (1720).

Protea aurea (Burm. f.) Rycroft ex Schutte in S. Afr. J. Sci. **69**: 57 (1973)—nom. nud.

Protea calycina Schneevoogt, Icon. Pl. Rar. t. 48 (1795). Type: Plate 48 in Schneevoogt, Icon. Pl. Rar.

Protea radiata Andr., Bot. Rep. t. 646 (1812). Type: Plate 646 in Andr., Bot. Rep.

- Protea latifolia* sensu Sims in Curtis's Bot. Mag. **42**: t. 1717 (1815).
- Protea radiata* Bonpl., Desc. Pl. Rar. Malmaison et Navarre: 144 t. 59 (1816). Type: Plate 59 in Bonpl. Desc. Pl. Rar. Malmaison et Navarre.
- Protea ovata* Thunb. in Mem. Acad. Imp. Sci. St. Petersbourg Hist. Acad. **6**: 548 t. 17 (1818). Type: E. cap. b. Spei, *Sparrman* s.n., sheet 2948 in herb. Thunberg (UPS!)
- Leucospermum ovatum* (Thunb.) Roem. & Schult., Mant. Syst. Veg. **3**: 266 (1827). Type: As for *Protea ovata* Thunb.
- Erodendrum aemulum* Salisb. ex Knight, Cult. Prot.: 38 (1809). Type: Attaquas Kloof, *Niven* 35 (K, holo.!)
- Protea longiflora* Lam. var. *latifolia* Klotzsch in Krauss, in Flora **28**: 76 (1845)—nom. nud. but based on: Ad sylv. margines prope Georgetown Jan. 1838, *Krauss* s.n. (NBG ex Acad. Hohenheim!)
- Protea longiflora* Lam. var. *ovalis* Phill. in Fl. Cap. **5**: 577 (1912). Type: Ex hort. Glasgow Bot. Gdn., without collector (K, holo.!)

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STUDIES IN THE GENUS *CERATIUM* SCHRANK WITH REFERENCE TO SPECIMENS COLLECTED IN THE AGULHAS CURRENT: 3.

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ABSTRACT

A taxonomic account is given of Subsection *Macroceras* Ostf., incorporating the use of polar co-ordinate measurements of antapical horn curvature in descriptions and delimitation of species.

UITTREKSEL

STUDIES IN DIE GENUS *CERATIUM* SCHRANK MET VERWYSING NA MONSTERS IN DIE AGULHASSTROOM VERSAMEL: 3.

'n Taksonomiese verslag van die subseksie *Macroceras* Ostf. wat polêre koördinate van antapikale horing geboëndheid in die beskrywing en afbakening van die soorte gebruik.

INTRODUCTION

The use of polar co-ordinates in measurement of antapical horn curvature in Section *Macroceras* Ostfeld has already been discussed, (Reinecke 1973). For convenience the terminology used in the key and descriptions is again given.

TERMINOLOGY

Polar co-ordinates—degree and radius co-ordinates used here as a means of measuring the curvature of the antapical horns, plotted on camera lucida drawings of full dorsal or ventral aspect, at intervals of 15 μ , along the edges of the horns initially adjacent to the base of the hypotheca.

Radius unit—on the scale of the camera lucida drawings and the polar co-ordinate graph paper used, one radius unit is approximately equal to 3 μ . The radius units are sometimes given as R.U.

Zero point for radius co-ordinates—the point of inception of the antapical horn immediately adjacent to the base of the hypotheca.

Posterior line—a line drawn to pass through the zero points of the antapical horns.

Zero line for degree co-ordinates—determined by drawing lines through the zero points of the right and left horns perpendicular to the posterior line.

MRC—the maximum rate of change of direction of curvature of a horn

measured in degrees over $15\ \mu$ after the initial curvature from $0-15\ \mu$. (Very rarely, the MRC occurs over two, in exceptional cases three, successive $15\ \mu$ intervals.)

MBC—the point of maximum backward curvature of the horns, determined by the construction of a tangent to the posterior or lower edge of the antapical horn parallel to the posterior line.

$\frac{B}{H}$ —ratio in which *H* is the perpendicular distance between a line joining the profile edges of the lower girdle list and a line parallel to it through the zero point for the radius co-ordinates of the left horn, and *B* is the perpendicular distance between this latter line and a line parallel to it drawn as a tangent to the lower edge of the left antapical horn.

$\frac{L90}{D}$ and $\frac{R90}{D}$ —ratios in which *L90* and *R90* are the left and right horn radius co-ordinates with the 90° co-ordinate, and *D* is the girdle diameter measured in radius units.

$\frac{RMBC}{D}$ —ratio in which *RMBC* is the right horn MBC radius co-ordinate in R.U.

In order to compare specimens illustrated in the literature with those seen in the Agulhas current NGY samples collected during International Geophysical Year 1958, it was necessary to make photographic enlargements at a scale similar to that of camera lucida drawings of the NGY specimens. In some cases the scale of the figures was unknown and it was impossible to estimate the girdle diameter, in other instances the scales could have been inaccurate and sometimes the drawings were poor.

Subgenus *ORTHOCERATIUM* Sournia (1967): 376.

Section *MACROCERAS* Ostenfeld (1903): 192.

Subsection *MACROCERAS*

DIAGNOSIS

Differs from Subsection *Robusta* Karsten in that chain formation is extremely rare, and the length of the apical horn in posterior members of a chain is greater than 0.4 times that of the anterior cell in a complete chain. Differs from Subsection *Reflexa* (Jörg.) Reinecke in that both antapical horns are anteriorly directed after the initial backward curvature.

KEY, USING POLAR CO-ORDINATE MEASUREMENTS OF ANTAPICAL HORN CURVATURE IN CAMERA LUCIDA DRAWINGS, TO TAXA OF SUBSECTION *MACROCERAS*.

(Based on specimens seen in Agulhas current NGY samples, sample IGY 121, from Oslo Fiord and on figures from the literature.)

I. Both antapical horns very obviously deflected ventrally

(1) Right horn MBC radius co-ordinate $\geq 60\ \mu$

C. deflexum f. sinensis

- (2) Right horn MBC radius co-ordinate $< 55 \mu$
 (i) Sum of left and right horn MRC's $> 50^\circ$ *C. deflexum f. deflexum*
 (ii) Sum of left and right horn MRC's $< 50^\circ$ *C. deflexum f. deflectomassum*
- II. Ventral deflexion of antapical horns slight or not possible to determine
- A. Left horn MRC occurs beyond the 75μ radius co-ordinate
- (1) Left horn degree co-ordinate with 15μ radius co-ordinate ≥ 90
 (i) Girdle diameter $\geq 60 \mu$ *C. massiliense var. massiliense**
 (ii) Girdle diameter $\leq 57 \mu$ *C. tenue**
- (2) Left horn degree co-ordinate with 15μ radius co-ordinate < 90
 (i) Left horn MBC degree co-ordinate $\geq 70^\circ$
 (a) Right horn MBC degree co-ordinate $\leq 40^\circ$ *C. deflexum f. sinensis*
 (aa) Right horn MBC degree co-ordinate $> 40^\circ$
 (b) Girdle diameter $< 45 \mu$ *C. trichoceros var. trichoceros*
 (bb) Girdle diameter $> 48 \mu$ *C. trichoceros var. contrarium*
 (bbb) Girdle diameter $45-48 \mu$
 (c) "Kink" present at base of left horn and/or ratio

$$\frac{RMBC}{D} > 1,75$$
 C. trichoceros var. trichoceros
 (cc) "Kink" absent from base of left horn and ratio

$$\frac{RMBC}{D} < 1,75$$
 C. trichoceros var. contrarium
- (ii) Left horn MBC degree co-ordinate $< 70^\circ$
 (a) Left horn MBC degree co-ordinate ≥ 65
 (b) Right horn MBC degree co-ordinate > 40
 (c) Girdle diameter $> 45 \mu$ *C. macroceros*
 (d) Right horn MRC $> 10^\circ$
 (dd) Right horn MRC $< 10^\circ$
 (e) Sum of left and right horn MRC's $> 25^\circ$ *C. macroceros*
 (ee) Sum of left and right horn MRC's $< 25^\circ$ *C. massiliense var. carriense**
- (cc) Girdle diameter $\leq 45 \mu$
 a. Girdle diameter $< 45 \mu$ *C. trichoceros var. trichoceros*
 aa. Girdle diameter $= 45 \mu$
 β . "Kink" present at base of left horn and/or ratio

$$\frac{RMBC}{D} \wedge 1,75$$
 C. trichoceros var. trichoceros
 $\beta\beta$. "Kink" absent from base of left horn and ratio

$$\frac{RMBC}{D} < 1,75$$
 C. trichoceros var. contrarium
- (bb) Right horn MBC degree co-ordinate ≤ 40
 a. Difference between left and right horn MBC degree co-ordinates $\leq 20^\circ$ *C. macroceros*
 aa. Difference between left and right horn MBC degree co-ordinates $\geq 20^\circ$
 β . Sum of left and right horn MRC's $> 40^\circ$, antapical horns smooth or with very minute denticles *C. deflexum f. sinensis*
 $\beta\beta$. Sum of left and right horn MRC's $< 40^\circ$, antapical horns often very spiny *C. macroceros*
- (aa) Left horn MBC degree co-ordinate $< 65^\circ$
 a. Ratio $\frac{L90}{D} \geq 2,00$ *C. macroceros*
 aa. Ratio $\frac{L90}{D} < 2,00$
 β . Difference between left and right horn MBC degree co-ordinates $\leq 20^\circ$ *C. macroceros*
 $\beta\beta$. Difference between left and right horn MBC degree co-ordinates $> 20^\circ$ *C. deflexum f. sinensis*
- AA. Left horn MRC occurs before the 75μ radius co-ordinate
- B. Ratio $\frac{B}{H} < 0,90$
- C. Ratio $\frac{B}{H} \geq 0,80$

- (1) Sum of left and right horn MRC's $\geq 40^\circ$
 - (i) Sum of left and right horn MRC's $> 50^\circ$
 - (a) Left horn degree co-ordinate with 105μ radius co-ordinate $\geq 150^\circ$ *C. deflexum f. deflexum*
 - (aa) Left horn degree co-ordinate with 105μ radius co-ordinate $< 150^\circ$
 - (b) Right horn degree co-ordinate with 105μ radius co-ordinate $< 115^\circ$ and difference between left and right horn MBC degree co-ordinates $\leq 20^\circ$ *C. macroceros**
 - (bb) Right horn degree co-ordinate with 105μ radius co-ordinate $> 115^\circ$ and/or difference between left and right horn MBC degree co-ordinates $> 20^\circ$ *C. deflexum f. deflexum*
 - (ii) Sum of left and right horn MRC's $\leq 50^\circ$ *C. deflexum f. deflectomassum*
 - (2) Sum of left and right horn MRC's $< 40^\circ$
 - (i) Left horn degree co-ordinate with 150μ radius co-ordinate $> 130^\circ$ *C. massiliense var. massiliense*
 - (ii) Left horn degree co-ordinate with 150μ radius co-ordinate $< 130^\circ$ *C. massiliense var. carriense*
- CC. Ratio $\frac{B}{H} < 0,80$
- (1) Right horn degree co-ordinate with 15μ radius co-ordinate $\geq 45^\circ$
 - (i) Girdle diameter $\leq 57 \mu$ *C. tenue*
 - (ii) Girdle diameter $\geq 60 \mu$
 - (a) Left horn degree co-ordinate with 150μ radius co-ordinate $> 130^\circ$ *C. massiliense var. massiliense*
 - (aa) Left horn degree co-ordinate with 150μ radius co-ordinate $< 130^\circ$ *C. massiliense var. carriense*
 - (2) Right horn degree co-ordinate with 15μ radius co-ordinate $< 45^\circ$
 - (i) Sum of left and right horn MRC's $\geq 40^\circ$
 - (a) Left horn degree co-ordinate with 150μ radius co-ordinate $< 130^\circ$ *C. massiliense var. carriense**
 - (aa) Left horn degree co-ordinate with 150μ radius co-ordinate $> 135^\circ$
 - (b) Sum of left and right horn MRC's $> 50^\circ$ *C. deflexum f. deflexum*
 - (bb) Sum of left and right horn MRC's $\leq 50^\circ$ *C. deflexum f. deflectomassum*
 - (ii) Sum of left and right horn MRC's $< 40^\circ$
 - (a) Left horn degree co-ordinate with 150μ radius co-ordinate $> 130^\circ$ *C. massiliense var. massiliense*
 - (aa) Left horn degree co-ordinate with 150μ radius co-ordinate $< 130^\circ$ *C. massiliense var. carriense*
- BB. Ratio $\frac{B}{H} \geq 0,90$
- (1) Ratio $\frac{B}{H} < 1,10$
 - (i) Right horn MRC $\leq 10^\circ$
 - (a) Girdle diameter $\geq 60 \mu$
 - (b) Sum of left and right horn MRC's $> 25^\circ$ *C. macroceros**
 - (bb) Sum of left and right horn MRC's $< 25^\circ$ *C. massiliense var. carriense*
 - (aa) Girdle diameter $< 57 \mu$ *C. macroceros**
 - (ii) Right horn MRC $> 10^\circ$
 - (a) Left horn degree co-ordinate with 105μ radius co-ordinate $\geq 150^\circ$
 - (b) Right horn MBC radius co-ordinate $\geq 60 \mu$ *C. deflexum f. sinensis*
 - (bb) Right horn MBC radius co-ordinate $< 55 \mu$
 - (c) Sum of left and right horn MRC's $> 50^\circ$ *C. deflexum f. deflexum*
 - (cc) Sum of left and right horn MRC's $\leq 50^\circ$ *C. deflexum f. deflectomassum*
 - (aa) Left horn degree co-ordinate with 105μ radius co-ordinate $< 150^\circ$

- a. Difference between left and right horn MBC degree co-ordinates $\leq 20^\circ$
- β . Right horn degree co-ordinate with $105\ \mu$ radius co-ordinate $> 115^\circ$ *C. deflexum f. deflexum*
- $\beta\beta$. Right horn degree co-ordinate with $105\ \mu$ radius co-ordinate $< 115^\circ$ *C. macroceros*
- aa. Difference between left and right horn MBC degree co-ordinates $> 20^\circ$
- (i) Left horn degree co-ordinate with $105\ \mu$ radius co-ordinate $> 135^\circ$
- (†) Right horn MBC radius co-ordinate $\geq 60\ \mu$ *C. deflexum f. sinensis**
- (++) Right horn MBC radius co-ordinate $< 55\ \mu$
- (*) Sum of left and right horn MRC's > 50 *C. deflexum f. deflexum*
- (**) Sum of left and right horn MRC's $\leq 50^\circ$ *C. deflexum f. deflectomassum**
- (//) Left horn degree co-ordinate with $105\ \mu$ radius co-ordinate $< 135^\circ$ *C. macroceros*
- (2) Ratio $\frac{B}{H} = \geq 1.10$ but < 1.50
- (i) Difference between left horn radius co-ordinates of tangent parallel to girdle and of point of MBC $> 100\ \mu$ *C. massiliense var. carriense*
- (ii) Difference between left horn radius co-ordinates of tangent parallel to girdle and of point of MBC $< 100\ \mu$
- (a) Right horn MRC $< 10^\circ$ and sum of left and right horn MRC's < 25 *C. massiliense var. carriense*
- (aa) Right horn MRC $> 10^\circ$, sum of left and right horn MRC's rarely $> 25^\circ$, never $< 20^\circ$
- (b) Left horn degree co-ordinate with $105\ \mu$ radius co-ordinate ≥ 150
- (c) Difference between left and right horn MBC degree co-ordinates $< 10^\circ$ *C. macroceros**
- (cc) Difference between left and right horn MEC degree co-ordinates $> 15^\circ$ *C. deflexum f. deflexum**
- (bb) Left horn degree co-ordinate with $105\ \mu$ radius co-ordinate < 150 *C. macroceros*
- (3) Ratio $\frac{B}{H} \geq 1.50$ *C. macroceros*

Ceratium macroceros (Ehrenberg) Vanhoeffen (1897): 310, 382, Pl. 5, Fig. 10. Okamura & Nishikawa (1904): 122, Pl. 6, Fig. 2; Paulsen (1908): 81, Fig. 109 (= Bergh (1882) Fig. 27); Jörgensen (1911): 63, Pl. 1, Fig. 6 (heteromorphic chain), Pl. 7, Figs. 132a, b, 133; Mangin (1912): 25, Fig. 10; Dangeard (1926): 315, Fig. 4c; Abé (1927): 427, Fig. 44A–E; Peters (1932): 47, Pl. 4, Fig. 17b; Wang (1936): 160, Fig. 29; Schiller (1937): 428, Fig. 468a, b (heteromorphic chain), ?c and ?d (solitary heteromorphs), (from Peters, reference not given); Silva (1949): 360, Pl. 7, Fig. 2, Pl. 9, Fig. 11; Margalef & Duran (1953): 42, Fig. 12a–e, ?f (solitary heteromorph); López (1966): 330, Fig. 16. ? e.p. Lebour (1925): 155, non Pl. 35, Fig. 1 (= *C. tenue* O. & S.); ? e.p. Wood (1954): 310, non Fig. 238a (either *C. massiliense var. massiliense* (Gour.) Kars. or *C. deflexum f. deflectomassum* Rein.); ? e.p. Klement (1964): 357, non Pl. 3, Fig. 1 (= *C. deflexum f. deflectomassum*).

* Indicates a single specimen recorded with these dimensions. The portions of the key in italics are included for the sake of completion, as specimens with these dimensions were not measured.

Non Ostenfeld & Schmidt (1901): 167, Fig. 19 (= *C. deflexum* f. *deflexum* (Kof.) Jörg.); *non* Wailes (1928) Pl. 11, Figs. 16–18 (= *C. tenue* and *C. longipes* (Bail.) Gran); *non* Ballantine (1961): 225, Fig. 56 (Either *C. deflexum* f. *deflectomassum* or *C. massiliense* var. *massiliense*).

Mentioned without illustration as *C. macroceros* by: Pavillard (1905): 53; (1907): 225; (1931): 87; Schröder (1906); Forti (1922): 62; Dangeard (1927): 377; Gaarder (1954): 14; Silva (1956); (1960); Braarud, Foyne & Hasle (1958); Travers and Travers (1962): 58; Mulford (1963): 86; Wood (1963): 12; Taylor (1967): 463; Nel (1968); Thornington Smith (1969); (1971); Hasle (1969): 152. "*C. macroceros* Ehrb. f." Okamura (1907): 128, Pl. 4, Fig. 19.

"*C. macroceros* (Ehrb.) f.?" Abé (1927): 428, Fig. 46.

Non "*C. macroceros* Ehrb. f.?" Okamura (1907): 128, Pl. 4, Fig. 20a, b (= *C. deflexum* f. *deflexum*).

C. macroceros subsp. *macroceros*: Graham & Bronikowsky (1944): 37, Fig. 21F. *C. macroceros* var. *macroceros*: Sournia (1966): 1982; (1967): 460, Fig. 83 (= Jörgensen (1911) Fig. 133).

Peridinium macroceros Ehrenberg (1840): 201.

C. tripos Nitzsch var. *α Per. macroceros* (Ehr.) Claparède & Lachmann (1859): 397, Pl. 19, Fig. 1.

C. tripos var. *macroceros*: Gourret (1883): 26, Pl. 2, Fig. 41; Cleve (1897): 301, Pl. 1, Fig. 6; ? Schröder (1900): 15, Pl. 1, Fig. 17f (peculiar form with unusually long right horn MBC radius co-ordinate).

Listed without figure as *C. tripos* var. *macroceros* by: Zacharias (1906): 543. *C. tripos macroceros*: Entz (1902): 100, e.p., Pl. 2, Fig. 15, ?13, ?14 (solitary heteromorphs), ?16 (only body and bases of horns shown), *non* 17 and 18 (= *C. massiliense* var. *massiliense*); Karsten (1906): 145, ep., Pl. 22, Fig. 29b–d, *non* a (= *C. massiliense* var. *massiliense*); (1907): 411, e.p., Pl. 49, Fig. 27b, *non* d (= *C. massiliense* var. *carriense* (Gour.) Rein.).

C. macroceros var. *karstenii* Abé (1927): 427, Fig. 45.

C. macroceros var. *gallicum* (Kofoid) Sournia (1966): 1982; (1967): 462, Fig. 84; Steidinger & Williams (1970): 46, Fig. 29a, b.

"*C. macroceros* var. *gallicum* (Kof.) Jörg." Schiller (1937): 430, Fig. 469 (= Jörgensen (1911) Fig. 134); Rampi (1939): 310, Fig. 42; Halim (1960): 180, Pl. 5, Fig. 7.

Mentioned without illustration as "*C. macroceros* var. *gallicum* (Kof.) Jörg." by: Gaarder (1954): 14; Klement (1964): 358.

Mentioned without illustration as "*C. macroceros* var. *gallicum*" by: Nel (1968). "*C. macroceros* f. *gallicum* (Kof.) Jörg." Halim (1963): 498, Fig. 27.

C. macroceros subsp. *gallicum* (Kof.) Jörgensen (1911): 63, Pl. 7, Figs. 134, 135; (1920): 83, Fig. 77; Forti (1922): 64, Pl. 3, Fig. 48 (= Jörgensen (1911) Fig. 134); Abé (1927): 429, Fig. 47A–D; Paulsen (1930): 87, Fig. 54A–C; Böhm (1931b):

38, Fig. 35a; Steemann Nielsen (1934): 25, Fig. 59; Graham & Bronikowsky (1944): 37, Fig. 21B, D, E *non* C (= *C. deflexum* f. *deflectomassum*); Wood (1954): 311, Fig. 238b.

Mentioned without illustration as *C. macroceros* *subsp. gallicum* by: Schröder (1911): 646; Böhm (1931a): 364; Pavillard (1931): 88; Steemann Nielsen (1939): 14; Silva (1949): 360; (1956).

C. macroceros "*gallicum* > *macroceros*" Sournia (1967): 464, Fig. 85.

C. macroceros "*macroceros*—*gallicum*" Sournia (1966): 1982.

C. gallicum Kofoid (1907b): 302, Pl. 24, Figs. 10–12.

Mentioned without illustration as *C. gallicum* by: Wood (1963): 9.

C. tripos macroceras *var. crassa* Karsten (1907): 411, e.p., Pl. 49, Fig. 27c, *non* a, e (= *C. massiliense* *var. massiliense* and *var. carriense*).

Mentioned with illustration as *C. macroceros* *var. crassa* by: Nel (1968).

C. tripos macroceras *var. tenuissima* Karsten (1907): 411, Pl. 49, Fig. 28a–e.

Mentioned without illustration as *C. macroceros* *var. tenuissima* by: Nel (1968).

C. tripos scoticum Schütt (1892): 266, 302, e.p., Fig. 76 IVc *non* Fig. 91 IV (unidentifiable with certainty—Jørgensen (1911) considered it as possibly *C. intermedium* (Jörg.) Jörg. = *C. tenue*).

Non C. tripos macroceras f. *scotica*: Schröder (1900): 15, Pl. 1, Fig. 17g (= *C. massiliense* *var. massiliense*).

C. tripos: Bergh (1882): 204, e.p., Pl. 14, Fig. 27; Hensen (1887) p.p., Pl. 6, Fig. 58; *non C. tripos* (Müller) Nitzsch.

C. ostenfeldii Kofoid (1907b): 305, e.p., Pl. 26, Fig. 24, *non* 22, 23, 25 (= *C. massiliense* *var. massiliense* and *var. carriense*).

C. hundhausenii: Pavillard (1931): 92, Pl. 3, Fig. 7; *non C. hundhausenii* Schröder (= *C. massiliense* *var. carriense*)

? *C. macroceros* *subsp. gallicum* f. *californiense* (Kof.) Jørgensen (1911): 64, Pl. 7, Figs. 136, 137; (1920): 89, Fig. 80 (all solitary heteromorphs); Forti (1922): Pl. 3, Fig. 49 (= Jørgensen Fig. 137).

? *C. macroceros* f. *californiense*: Halim (1960): 180, Pl. 5, Fig. 6 (solitary heteromorph).

? *C. californiense* Kofoid (1907b): 302, Pl. 23, Figs. 6–9; (1908a): 380, 382, Figs. 32, 33; Karsten (1907) Pl. 51, Fig. 15 (all solitary heteromorphs); Pavillard (1931): 88, Pl. 3, Fig. 2 (long horned cell).

? *Non C. macroceros* *var. hainanensis* Nie (1936): 62, Fig. 28A, B (? = *C. deflexum* f. *sinensis* Rein.).

Diagnosis: In the specimens examined, *C. macroceros* differs from *C. massiliense* *var. massiliense* (Gour.) Kars. and most specimens of *C. massiliense* *var. carriense* (Gour.) Rein. in that the ratio $\frac{B}{H}$ is $\geq 0,90$ (the single specimen of *C. macroceros* recorded from the Agulhas current in which this ratio was 0,83, differed from

C. massiliense in that the girdle diameter was 51μ); *C. macroceros* differs from the few specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is ≥ 0.90 , but always < 1.50 , in that the right horn MRC is generally $> 10^\circ$ and the sum of left and right horn MRC's is generally $> 25^\circ$; *C. macroceros* differs further from those specimens of *var. carriense* in which the ratio $\frac{B}{H}$ is > 1.10 , in that the difference between the left horn radius co-ordinates of the tangent, parallel to the girdle, to the lower edge of the antapical horn and of the point of MBC is $< 100 \mu$, mostly $< 50 \mu$; (the three specimens of *C. macroceros* recorded in which the right horn MRC was $\leq 10^\circ$, differed from *var. carriense* in that in the first, the ratio $\frac{B}{H}$ was 2.20, in the second the sum of left and right horn MRC's was 36° and in the third, girdle diameter was 54μ).

C. macroceros differs from *C. deflexum* (Kof.) Jörg. in lacking a marked ventral deflexion of the antapical horns; in terms of polar co-ordinate measurements of two-dimensional camera lucida drawings, *C. macroceros* differs from *C. deflexum f. deflexum* in that the left horn MRC often occurs beyond the 75μ radius co-ordinate; those specimens of *C. macroceros* in which the left horn MRC occurs before the 75μ radius co-ordinate, differ from most specimens of *f. deflexum* in that the left horn degree co-ordinate with the 105μ radius co-ordinate is $< 150^\circ$, mostly $< 145^\circ$; (the single specimen of *C. macroceros*, recorded from Oslo Fiord, in which this co-ordinate was 152° differed from *f. deflexum* in that the difference between left and right horn MBC degree co-ordinates was 7°); *C. macroceros* differs from those specimens of *f. deflexum* in which the left horn degree co-ordinate with the 105μ radius co-ordinate is $< 150^\circ$, in that the right horn degree co-ordinate with the 105μ radius co-ordinate is $< 115^\circ$ and the difference between the left and right horn MBC degree co-ordinates is $\leq 20^\circ$; (the two specimens recorded of *C. macroceros* in which this difference was $> 20^\circ$, (Abé (1920) Fig. 47c and Karsten (1907) Pl. 49, Fig. 27c), differed from *f. deflexum* in that the left horn degree co-ordinate with the 105μ radius co-ordinate was $< 135^\circ$ and the right horn degree co-ordinate with the 105μ radius co-ordinate was $< 100^\circ$). *C. macroceros* differs from *C. deflexum f. deflectomassum* Rein. in that the ratio $\frac{L_{90}}{D}$ is ≥ 0.90 and the difference between left and right horn MBC degree co-ordinates generally $\leq 20^\circ$; *C. macroceros* differs from *C. deflexum f. sinensis* Rein. in that the difference between left and right horn MBC degree co-ordinates is generally $\leq 20^\circ$ and the sum of left and right horn MRC'S is often $< 45^\circ$; (the two specimens recorded of *C. macroceros* in which the difference between the left and right horn MBC degree co-ordinates was $> 20^\circ$, differed from *f. sinensis* in that in the one, the sum of left and right horn MRC's was 31° , in the other the right horn MBC radius co-ordinate was $< 60 \mu$ and the girdle diameter about 53μ). *C. macroceros* differs further from *C. deflexum* in that far coarser and more prominent denticles or spines may occur along the lower margins of the antapical

horns in the region of recurvature, than are ever found in *C. deflexum*, and the girdle is often incompletely developed on the right side.

C. macroceros generally differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MBC degree co-ordinate is $< 70^\circ$; the few specimens of *C. macroceros* in which this co-ordinate is $\geq 65^\circ$, differ from the few specimens of *C. trichoceros* in which this co-ordinate is $\geq 65^\circ$, in that the girdle diameter is $> 55 \mu$, while in the specimens of *C. trichoceros* it is $\leq 45 \mu$.

C. macroceros differs from *C. tenue* O. & S. in that the left horn degree co-ordinate with the 15μ radius co-ordinate is $< 70^\circ$.

INTRODUCTION

C. macroceros is one of the commonest and most widespread species of Section *Macroceras* and yet the overall picture of its variation and distribution is not complete. It has been confused with *C. deflexum* and this is discussed under that species. It exhibits a variation in form correlated with a variation in temperature. Previous authors have regarded the warm water form as a discrete taxon. Sournia (1966) treated it as a variety, *var. gallicum* (Kof.) Sournia. Peters (1932) was the first to refer to it as a variety, but apparently unintentionally, as "die *var. gallicum* Kofoid." Similarly, Schiller (1937) referred to "*var. gallicum* (Kofoid) Jörg." and Halim (1963) to "*f. gallicum* (Kof.) Jörg."

Jørgensen (1911) considered '*C. macroceros subsp. gallicum* (Kof.) Jörg.' to differ from *subsp. macroceros* in being somewhat smaller and more delicate, with the right side of the girdle frequently indistinct or incompletely formed, the thecal structure usually not apparent, sometimes distinct in older specimens but much less developed than in *subsp. macroceros*, the antapical horns initially less divergent, their recurvature almost angular and the angle made by the forward recurvature of the right horn more or less smaller than 90° , (being mostly 90° or a little larger in *subsp. macroceros*). Graham & Bronikowsky (1944) noted that the body was longer in forms from the cold North Atlantic. Jørgensen gave the girdle diameter of *subsp. macroceros* as $48\text{--}57 \mu$ and of '*subsp. gallicum*' as $45\text{--}55 \mu$, exceptionally up to 70μ . He commented: "there is no character by which these two forms can be absolutely separated".

An examination of the range of form occurring in *C. macroceros* indicates that it is indeed impossible to divide this species into infraspecific taxa which are always distinct.

The cold water form was originally described from the Baltic, the warm water form from off San Diego, California. In the Agulhas current NGY samples, with one exception, only specimens resembling Kofoid's iconotype were found, but with the girdle incompletely formed and invisible plate sutures. The exception was a recently divided specimen from station NGY 41 (temperature from $50\text{--}0$ m, $16.66\text{--}17.49^\circ\text{C}$, see p. 352), with a girdle diameter of 51μ ,

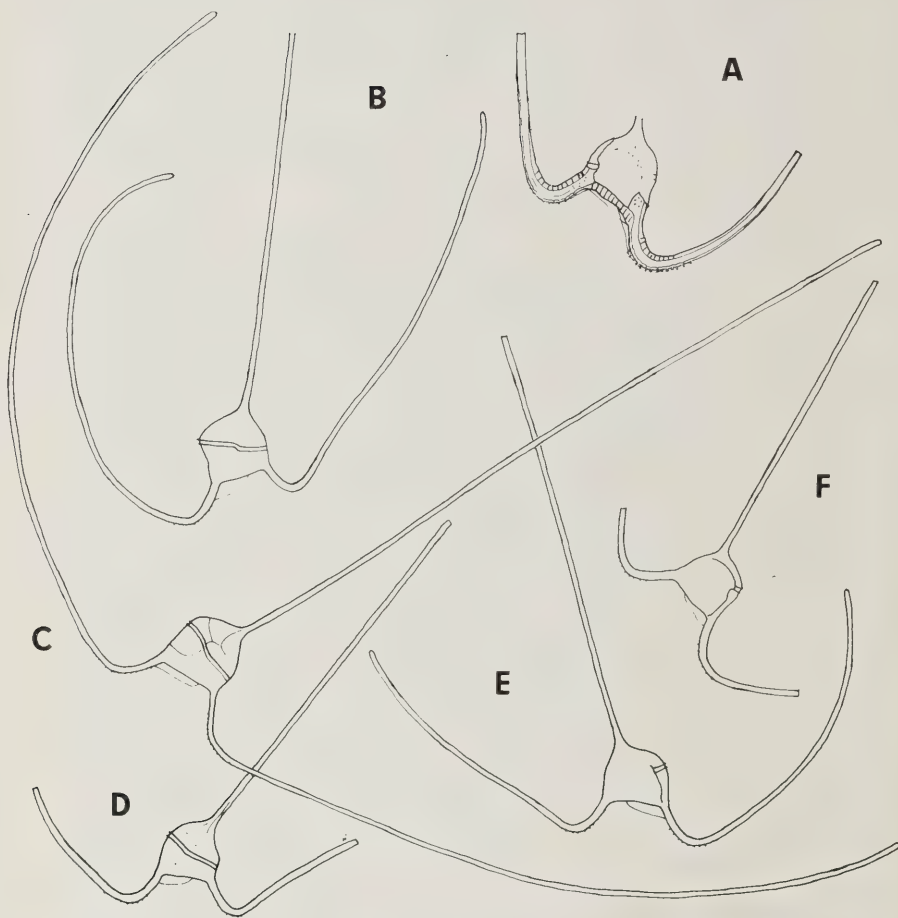


FIG. 1.

C. macroceros (Ehb.) Vanh.: Specimens from Agulhas current NGY stations. Girdle diameters: A 51 μ , B 48 μ , C 48 μ , D 40 μ , E 45 μ , F 45 μ ; A, recently divided specimen from station NGY 41 with thickened theca, thecal wall shown in optical section and surface view.

and a posterior half in which the theca was well developed with thickened walls and prominent spines supporting narrow lists along the lower margins of the antapical horns in the region of recurvature. (See Fig. 1).

Specimens were also examined from an NIOE station further South, NIOE 121 (40° 02' S, 29° 28' E, temperature from 100–0 m, 12.15–13.70 C, Shipley & Zoutendyk 1964) and from Oslo Fiord, (see Figs. 2 and 3). Relevant measurements of body size and antapical horn curvature of these specimens and of the iconotypes of Claparède & Lachmann (1859) and Kofoed (1907b) are shown in Figure 4.

In the Oslo specimens, the thecal wall is well developed with fairly coarse spines on the lower margins of the distal parts of the antapical horns, but the girdle is often incompletely formed on the right side; the left horn MRC occurs between the 60 and 105 μ radius co-ordinates and the antapical horns are re-curved forwards in a rounded curve, the girdle diameter is mostly 54–63 μ and the ratio body length/girdle diameter is mostly greater than 1.20. In the NGY specimens, the thecal wall is more delicate, the antapical horns thinner, usually with minute spines in the region of recurvature, the left horn MRC occurs between the 30 and 60 μ radius co-ordinates, and the antapical horns are re-curved forwards in an angled curve; the girdle diameter is mostly 42–48 μ and the length/breadth ratio does not exceed 1.20. There is no difference in the initial divergence of the antapical horns between specimens from the two localities. The angle made by the forward recurvature of the right horn usually approximates a "rounded" right angle in the Oslo Fiord specimens, and an "angled" right angle in those from the Agulhas current.

The NIOE specimens are in all respects intermediate in character between those from the Oslo Fiord and from the NGY Agulhas current samples, making it impossible to place the three groups of specimens in anything but the same taxon.

DISTRIBUTION AND VARIATION AS DESCRIBED IN THE LITERATURE: Ocean currents and their seasonal variation complicate an investigation of the distribution of planktonic taxa which vary morphologically with temperature changes, but an examination of the literature indicates that the differences between the cold and warm water forms of *C. macroceros*, with regard to both morphological variation and distribution with reference to temperature, are not clear cut, and that the species varies more than indicated in Jörgensen's description of 1911.

Jörgensen gave the girdle of the cold water '*subsp. macroceros*' as 48–57 μ and mentioned that the diameter of the warm water '*subsp. gallicum*' was exceptionally as much as 70 μ . The available evidence indicates that larger diameters are found in specimens outside the tropics. Diameters in excess of 60 μ and up to 70 μ have been recorded in specimens from the Atlantic and

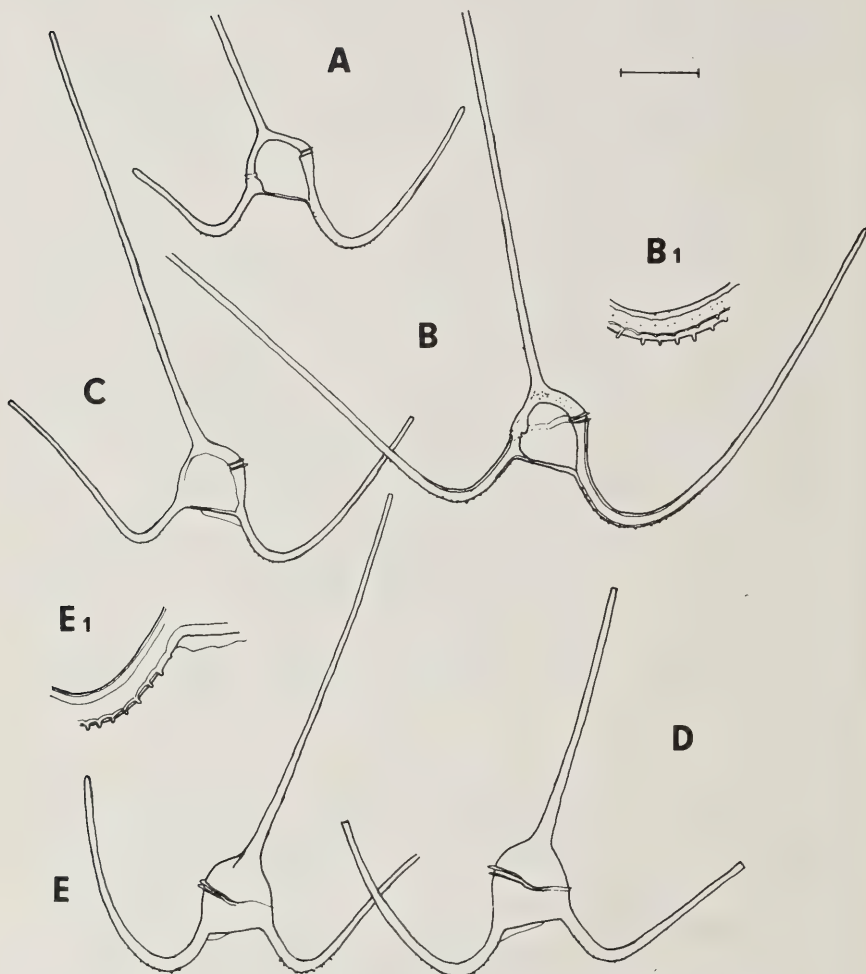


FIG. 2.

C. macroceros (Ehb.) Vanh.: Specimens from S.W. Indian Ocean station NIOE 121. In **B**, thecal wall seen in surface view and optical section; scale line represents $50\ \mu$; **B₁** and **E₁**, details of portion of left horn at a higher magnification, thecal wall shown in optical section.

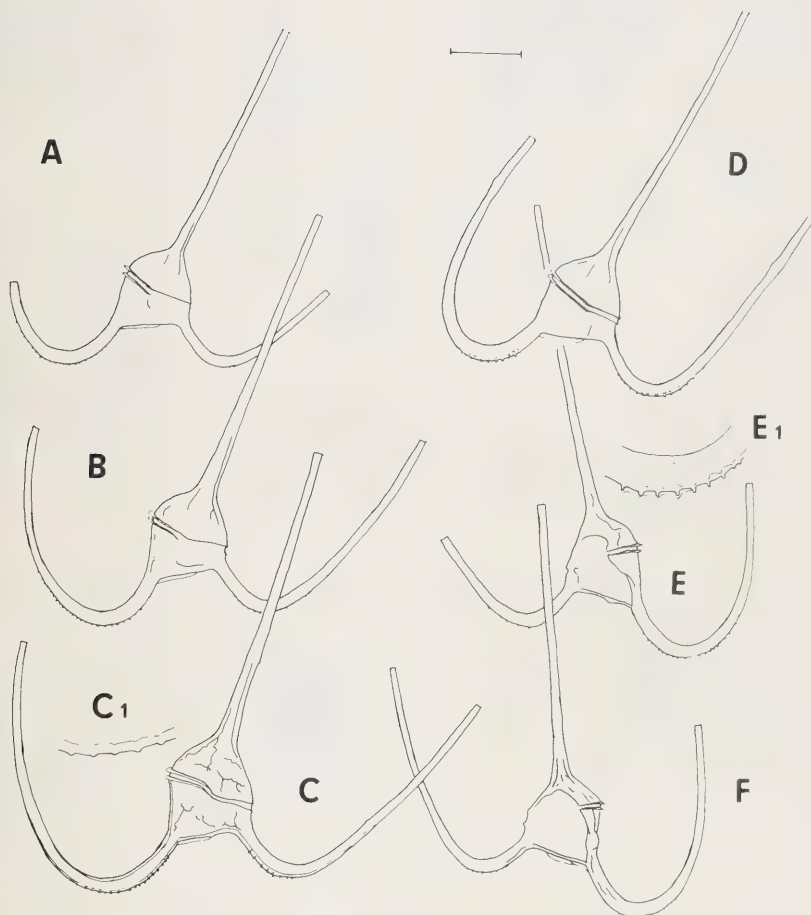


FIG. 3.

C. macroceros (Ehb.) Vanh.: Specimens from Oslo Fiord. In C, thecal wall seen in optical section and surface view; scale line represents 50 μ ; C1 and E1, details of portion of left horn at a higher magnification, thecal wall in optical section.

adjacent waters: from Oslo Fiord, the Shetland Isles (Vanhoeffen 1897*), near the Azores (under the name *C. hundhausenii*, Pavillard 1931*, treated as '*var. gallicum*' by Schiller, 1937), from Vigo (Margalef & Duran 1953) and the Mediterranean (Paulsen 1930, Rampi 1939*).

In the S. Atlantic, Peters reported both gigantic robust cells and delicate thin walled cells, the distribution of which showed no definite pattern. He found only robust forms in his "Transition area" (S. central Atlantic, between 37 and 45° S.). In the Indian ocean, two robust specimens, from an unspecified locality, presumably a cold water southern station, are depicted by Karsten (1907, Pl. 49, Figs. 27b and c, diameters estimated at 68 and 88 μ). In the Pacific and adjacent waters, large specimens are recorded from Mutsu Bay (Abé 1927, diameter 50–68 μ) and off San Diego (Kofoid 1907b, under the name *C. ostenfeldii*).

The highest values of the ratio $\frac{B}{H}$, in excess of 1.50, appear to be found in specimens from cooler waters, where, however, ratios of less than 1.00 are also recorded.

Graham (1941), who considered that there were no truly temperate oceanic ceratia, described '*C. macroceros subsp. macroceros*' as a subpolar taxon. This is misleading, for it implies a far greater difference between the cold and warm water forms of *C. macroceros* than exists. In fact, Sournia (1967) considered Graham & Bronikowsky's specimen of '*subsp. macroceros*' from S.E. of Greenland (1944, Fig. 21F) to be intermediate between '*var. macroceros*' and '*var. gallicum*'.

Atlantic ocean: In the Atlantic there appears to be no discontinuity in the variation, but a gradual change in appearance associated with a change in temperature. Pavillard (1931) wrote of '*subsp. gallicum*': "Remplace le type dans les mers tempérées et chaudes, sans qu'il soit possible de tracer une démarcation territoriale absolue". Graham & Bronikowsky found, with two exceptions, that '*subsp. macroceros*' was only recorded from Carnegie N. Atlantic stations North of latitude 40°, while Mangin recorded what he named as *C. macroceros* from 25–77°N. The three specimens he figures have the ratio $\frac{B}{H}$ of about 1.80–1.86. Silva (Bay of Cascais, 1949) and Margalef & Duran (Vigo, 1953) found both what they considered to be '*subsp. gallicum*' and '*subsp. macroceros*' in Iberian Atlantic waters. One of the specimens depicted by Silva (l.c. Pl. 9, Fig. 11) resembles specimens from NIOE 121, except that the distal parts of the antapical horns are less spreading. Margalef & Duran gave the diameter of '*subsp. gallicum*' (l.c. Fig 12c–e) as 45–53 μ , and of the form "Quiza . . . corresponde al tipo de la especie" (l.c. Fig. 12a, b) as 54–70 μ . The specimen in Fig. 12b is intermediate in character between the specimens of Figs. 12a and 12c.

Jørgensen (1911) published two figures of '*subsp. macroceros*' from Bergen,

* Calculated from scale of figure.



FIG. 4A

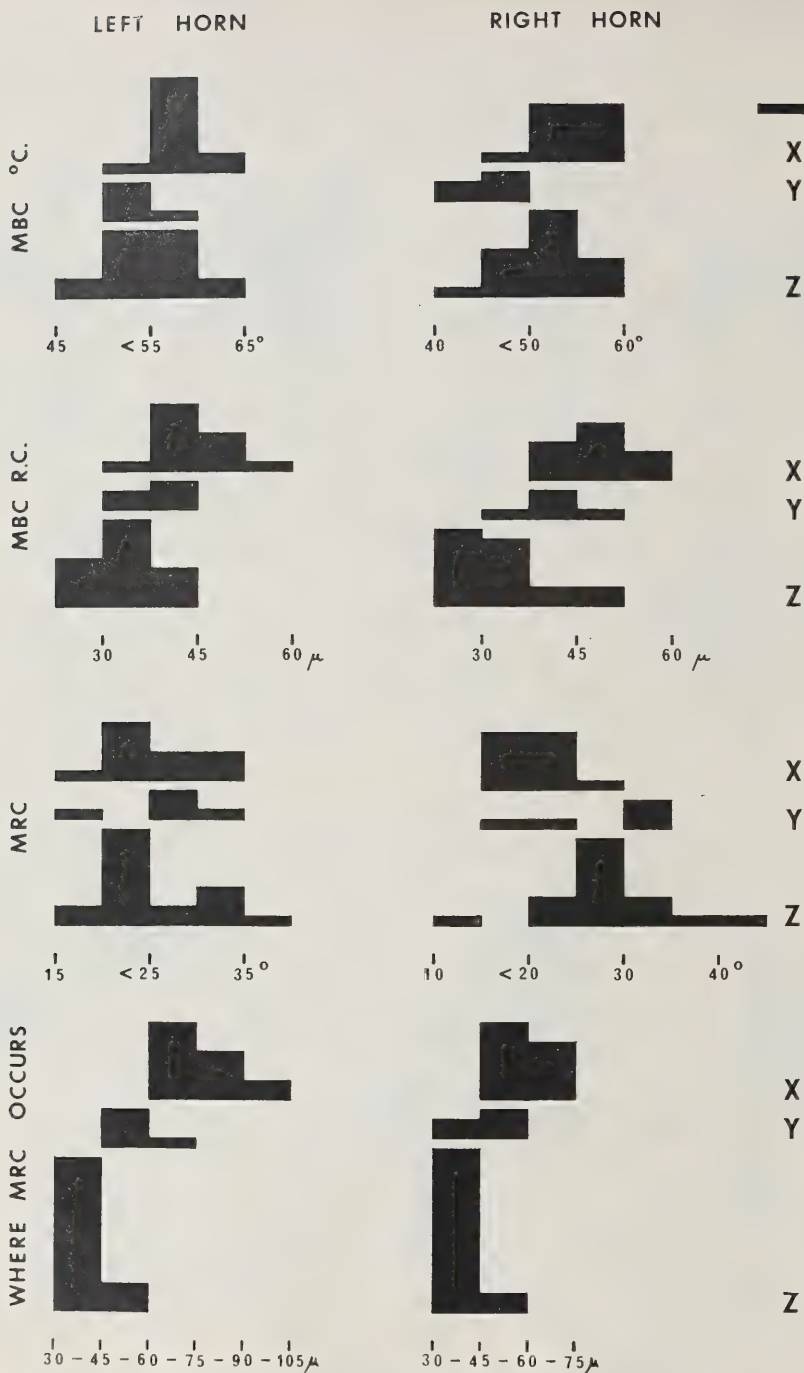


FIG. 4B

one of which (l.c. Fig. 133) agrees well with a figure of Bergh (1882), reproduced in Paulsen's "Peridiniales" (1908) as *C. macroceros*, the other with an incomplete girdle, (l.c. Fig. 132a) is in many respects intermediate between Fig. 133 and a figure of a specimen of '*subsp. gallicum*' from the Azores (l.c. Fig. 135).

The only figure of a specimen from the S. Atlantic appears to be that of Peters (1932), from a station off Cape Town, with an incomplete girdle, which resembles Kofoed's iconotype, but which Peters did not appear to recognise as such, describing it as a fairly distinctive form of *C. macroceros* characteristic of his "Agulhas area", although he had commented: "In dem Expeditionsgebiet wurde überwiegend die *var. gallicum* Kofoed angetroffen; nur im Süden . . . (between about 35 and 45°S) . . . wurden vornehmlich der Hauptform ähnliche Vertreter gefangen." He commented on the great variability of the species, and found it to be absent from his "Falkland area".

Mediterranean: Jörgensen (1920) considered that only '*subsp. gallicum*' was present in the Mediterranean. Pavillard (1907) had, however, written of specimens from the Gulf of Lyons: "parfaitement identiques au dessin classiques de Bergh". Forti (1922) reported specimens somewhat similar to Jörgensen's Fig. 132, and Böhm (1931a) noted that in the Adriatic '*subsp. gallicum*' "nahert sich oft beträchtlich der Hauptart". Paulsen (1930) found forms of '*subsp. gallicum*' with incomplete girdles and more robust forms with complete girdles in the Alboran Sea. In his figure of the latter, which Sournia (1967) considered to be intermediate between '*var. gallicum*' and '*var. macroceros*', the forward recurvature of the antapical horns is not angled. Rampi (1939) published a poor figure of '*var. gallicum* (Kof.) Jörg.' in which the girdle is complete, the forward recurvature of the antapical horns rounded, and the estimated diameter about 63 μ . The Travers (1962), in their account of the phytoplankton of the Gulf of Marseille, listed the species as *C. macroceros*, not differentiating '*var. gallicum* (Kof.) Jörg.'.

Indian Ocean and Australian Waters: Wood (1954) recorded both '*subsp. macroceros*' and '*subsp. gallicum*' from Australian waters, but his concept of the former appears to be confused, for the specimen illustrated has the ratio $\frac{B}{H} < 0.80$ (and is probably a specimen of *C. massiliense*), and he described its

FIG. 4A, B.

C. macroceros (Ehb.) Vanh.: A comparison of antapical horn curvature measured in polar co-ordinates, diameter and the ratio $\frac{L}{B}$, in specimens from Oslo Fiord (X), S.W. Indian Ocean station NIOE 121 (Y) and Agulhas current NGY samples (Z). LH °C = left horn degree co-ordinate, RC or R.C. = radius co-ordinate, L.H. and R.H. = left and right horns = $\frac{L}{B}$ length of body measured from base of outer edge of left horn to base of apical horn/girdle diameter. For other abbreviations, see text. The triangle above the X histograms indicates the measurements for the specimen in Claparède & Lachmann's iconotype, (enlarged assuming a girdle diameter of 57 μ), the triangles with the Z histograms indicate the measurements of the specimens in Kofoed's iconotype. The isolated black bar indicates one specimen.

distribution as "... Rarer in tropical waters, where it is replaced by *C. gallicum*". In his Indian Ocean Checklist (1963), he treated *C. gallicum* as a separate species and it is unlikely that his records for *C. macroceros* refer to the cold water form, for they are all from relatively warm waters, and some, eg. Ballantine (1961), refer wholly or in part to other species. The variation of *C. macroceros* in the S.W. Indian ocean as far South as latitude 40°, has been discussed. The only other records of forms from the Indian Ocean resembling cold water N. Atlantic forms, are the previously mentioned robust specimens depicted by Karsten (1907, Pl. 49, Figs. 27b and c). Steemann Nielsen recorded only '*subsp. gallicum*' in the Dana Indian ocean samples, but these did not extend South of latitude 36°. He described this taxon as "one of the most frequent ceratia, interoceanic, tropical-subtropical euphotic".

Pacific Ocean and East Asian waters: The only specimen of *C. macroceros* depicted in the literature from this area, which resembles Claparède & Lachmann's iconotype of the cold water form of *C. macroceros*, is that of Wang (1936) from the Gulf of Pê Hai (Gulf of Chili). Wang gives a diameter range of 43–48 μ , which is lower than given by Jörgensen, but in the specimen illustrated, the girdle is completely formed, the thecal wall is thickened with ridges, the antapical horns are coarsely toothed and recurved forwards in a rounded curve, the ratio body length/breadth is about 1.24 and the ratio $\frac{B}{H}$ about 1.93. Sournia (1967), however, considered this to be intermediate between '*var. gallicum*' and '*var. macroceros*'. Böhm (1931b) recorded *C. macroceros* from off the Eastern coast of Asia as "rather uncommon as *subsp. gallicum*" from a few stations South of latitude 25°. The specimen illustrated has a complete girdle and resembles Paulsen's Fig. 54A from the Mediterranean.

Specimens from Mutsu Bay, Japan, exhibiting a considerable range of variation are depicted by Abé (1927). Thecal structure is not shown, the girdle is mostly incomplete, diameter varies from 50–68 μ , the ratio body length/breadth is about 1.16–1.21, the ratio $\frac{B}{H}$ about 1.08–1.50 and the spread of the antapical horns is very variable. Forms with spreading horns, which most resemble Kofoid's iconotypes in horn curvature, were named *C. macroceros*, those with less spreading horns, the curvature of which in some instances resembled specimens referred to by other authors as '*subsp. macroceros*', were named '*subsp. gallicum*', and a form with a swollen body was named '*C. macroceros var. karstenii*', which Abé considered to be the same as Karsten's '*C. tripos var. crassa*' (1907, Pl. 49, Fig. 27e), here treated as *C. massiliense*. Sournia (1967) considered the specimens referred to by Abé as *C. macroceros* to be intermediate between '*var. gallicum*' and '*var. macroceros*'.

Steemann Nielsen (1934) recorded only '*subsp. gallicum*' from the Dana S. Pacific stations, where it was not observed in cold waters S.E. of New Zealand and in truly neritic stations. He noted a slight tendency for the diameter to

increase with a decrease in temperature. For example, at a station with a surface temperature of 26.9°C, only diameters of 42–45 μ were recorded, while at a station with a surface temperature of 21.0°C, diameters of 46–55 μ were recorded.

Graham & Bronikowsky (1944) recorded only '*subsp. gallicum*' from the N. Pacific Carnegie stations, where the N. limits were between latitudes 38 and 42°. They considered the absence of '*subsp. macroceros*' from the cold N. Pacific as indicative of the hydrological isolation of this part of the ocean. This again suggests a far greater difference between the cold and warm water forms of *C. macroceros* than is evident. They also noted that at most of the cold N. Pacific stations, the phosphate content of the water was generally above 100 mg PO₄/m³, while in the cold N. Atlantic samples where '*subsp. macroceros*' was found, the phosphate content was mostly below 50 mg/m³, and further, that '*subsp. gallicum*' was absent off Peru, where again the phosphate content was high. This factor appears to be more significant than they indicated. They considered that in the cold S. Pacific (the Southernmost Carnegie station being at about latitude 40°) "the species assumed the aspect of *subsp. macroceros*", but the specimen figured (l.c. Fig. 21C) most resembles *C. deflexum* f. *deflecto-massum*—it has the ratio $\frac{B}{H}$ about 0.56.

Hasle (1969) recorded *C. macroceros* from the Pacific Southern Ocean, but made no mention of its appearance.

The foregoing shows that, while the extreme warm and cold water forms of *C. macroceros* are recognisable, the presence of a continuous series of intermediates makes it impossible to divide the species into definable subspecific categories of even the lowest rank, and accordingly the infraspecific taxa of *C. macroceros* are discarded.

Culture experiments on the effects of phosphates and of temperature on forms from cold and warm waters would be of great interest. Also, more records of occurrence and variation of the species in cold Southern waters are needed.

Description

Thecal ornamentation: The girdle is often incompletely formed on the right side: seen dorsally, about halfway across the upper and lower girdle lists become smaller, so that on the right side they are reduced to ridges or are altogether absent, or only the upper list is present as a ridge; seen ventrally, on the right side of the sulcus the girdle is absent or very faintly indicated. Incomplete girdle development is more usually found in truly warm water specimens, and was the case in all Agulhas current specimens seen, but it is sometimes seen in specimens from cooler waters. In warm water specimens, the thecal walls are delicate and unridged, the antapical horns are slender and smooth, or with fine minute spines along the lower margins of the proximal parts; a single smooth margined to

slightly serrated list is present between the base of the left and horn and the hypotheca, extending about two thirds of the way across the hypotheca base. In cold water forms, the theca is thickened and ridged, and the antapical horns are thicker with coarser spines, which sometimes support a narrow list.

Horn length and disposition: Cold water specimens are often found with broken (or autotomised?) antapical horns, as was the case in those seen from Oslo Fiord and station NIOE 121, where in most specimens the horns only extended to the 105μ radius co-ordinate, and in no instance beyond the 225μ co-ordinate. In some of the Agulhas current NGY specimens, the antapical horns were long with tapered, rounded, sometimes slightly inflated, tips; in others, the horns were short, not exceeding the 105μ radius co-ordinate, with rounded truncate, abruptly truncate, in two instances slightly inflated, tips. In specimens with short horns with rounded tips it was not possible to determine whether the horns were short *ab initio* or whether they were broken or autotomised. Spread of antapical horns is variable, regardless of temperature, but truly cold water forms have not been recorded with as great a spread as sometimes seen in those from warm waters, and in cold water specimens the recurved distal part may lie roughly parallel to the apical horn. When the antapical horns are long, the ends appear to be slightly flexible, sometimes curving outwards. The bases of both antapical horns make an obvious angle with the base of the hypotheca. In typical warm water specimens, the forward recurvature of the more slender antapical horns is generally "angled", while in typical cold water specimens with thicker horns, it is "rounded".

Jørgensen (1911) wrote of the cold water '*subsp. macroceros*' that the right horn was "stark ventral gerichtet". This was not observed in specimens examined under the microscope, nor shown by Abé (l.c. Fig. 47B) in figures of apical and antapical views.

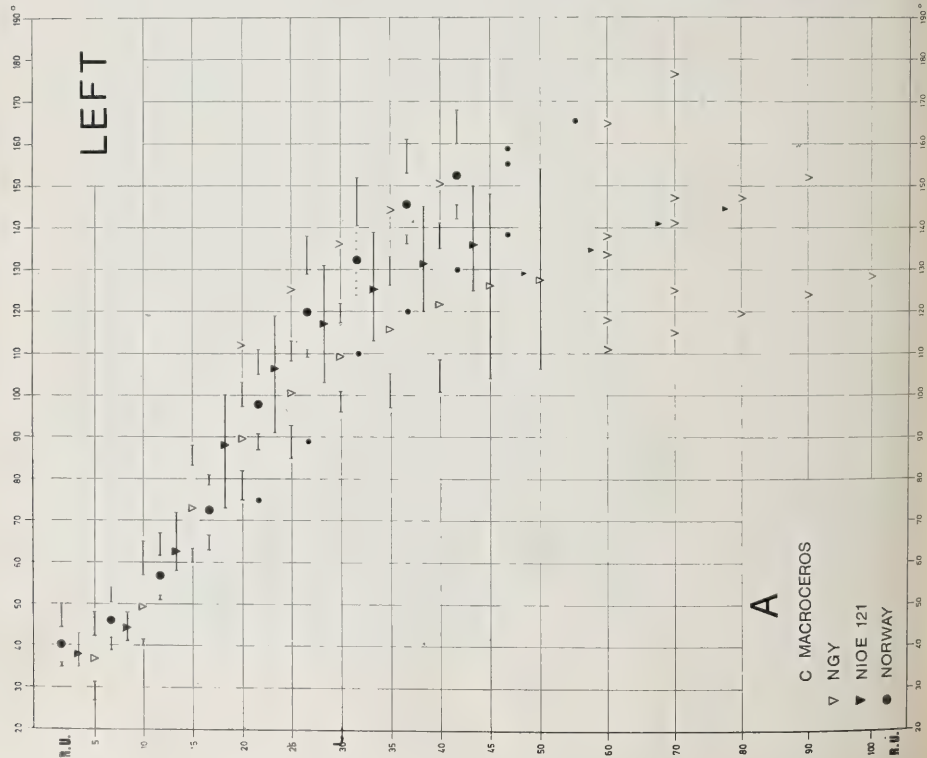
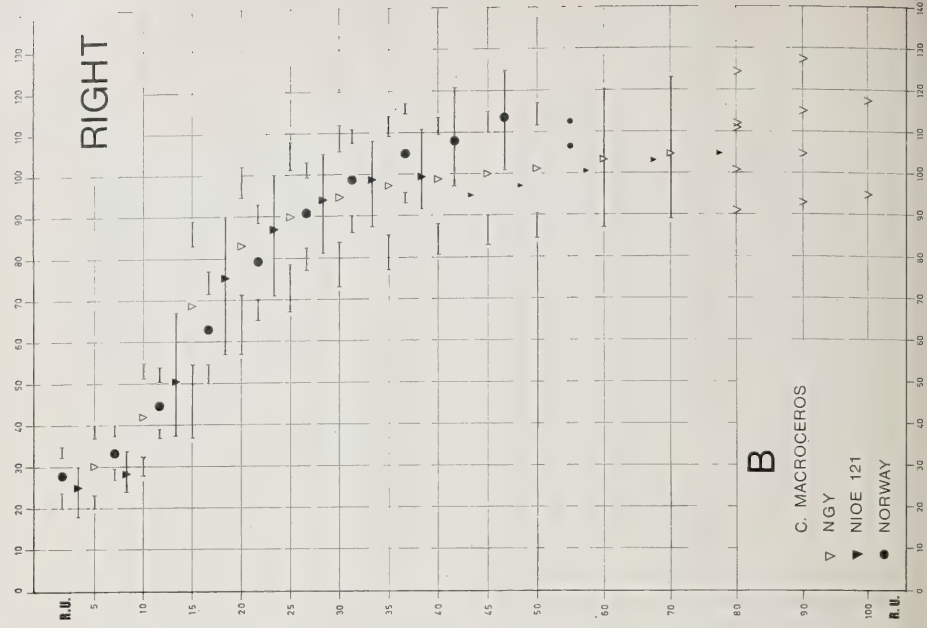
Mangin (1912) depicted a specimen in which the distal part of the apical horn was inflated.

Polar co-ordinate measurements of horn curvature: *Left horn:* degree co-ordinate with 15μ radius co-ordinate $27-60^\circ$, mostly $35-50^\circ$, not recorded above 50° in truly warm water forms; degree co-ordinate with 105μ radius co-ordinate variable, $88-152^\circ$, mostly $105-145^\circ$; with 150μ , $106-173^\circ$; with 300μ , $128-197^\circ$ in the few specimens seen with long horns; MBC degree co-ordinate $45-68^\circ$, mostly $50-60^\circ$; MBC radius co-ordinate $27-69\mu$, mostly $30-60\mu$, generally $< 38\mu$ in typical warm water forms and $> 38\mu$ in typical cold water forms and in the specimens with larger diameters figured by Paulsen (Alboran Sea, Mediterranean) and Abé (Mutsu Bay, Japan); MRC $10-35^\circ$, mostly $15-30^\circ$, occurring between 30 and 105μ radius co-ordinates, (between 120 and 135μ in Karsten's specimen, Pl. 49, Fig. 27c), generally before the 60μ co-ordinate in typical warm water forms and beyond it in typical cold water forms, (between 30 and 75μ

in Abé's specimens, and between 60 and 75 μ in those of Paulsen); $\frac{190}{D}$ 0.90–1.80 (as much as 2.18 in a specimen figured by Karsten (1907) Pl. 49, Fig. 28a); $\frac{H}{H+L}$ 0.90–2.22 (0.83 in only one instance), generally not exceeding 1.30 in warm water specimens (1.08–1.55 in Abé's figures, 1.66 in Paulsen's Fig. 58C). *Right horn*: degree co-ordinate with 15 μ radius co-ordinate 17–45°, (zero in Karsten's Pl. 49, Fig. 27c), mostly 17–37°, generally less than in the left horn by up to 32° (52° in Karsten's Fig. 27c), mostly by 1–25°, sometimes greater than in the left horn by up to 10°; degree co-ordinate with 105 μ radius co-ordinate variable, 72–114°, mostly 80–110°; with 300 μ , 94–124° in the few specimens seen with long horns; MBC degree co-ordinate 33–62°, mostly 40–55°, less than in the left horn by up to 25° (30° in Karsten's Fig. 27c), mostly by 1–15°, sometimes greater than in the left horn by up to 5°; MBC radius co-ordinate 26–83 μ , mostly < 42 μ in typical warm water forms and > 42 μ in typical cold water forms (also in the specimens figured by Abé and Paulsen); less than in the left horn by up to 20 μ , mostly by up to 5 μ , or greater than in the left horn by up to 32 μ , mostly by up to 15 μ ; MRC is 9–41°, mostly > 20° in typical warm water forms and < 23° in cold water forms (and the specimens figured by Abé and Paulsen); MRC occurs between 30 and 120 μ radius co-ordinates (between 15 and 30 μ in one small-diametered form), mostly between 30 and 45 μ in typical warm water forms, and beyond 45 μ in cold water forms (between 30 and 75 μ in Abé's specimens, and 45 and 75 μ in those of Paulsen); $\frac{R_{90}}{D}$ 0.96–4.55, mostly 1.25–2.50; sum of right and left horn MRC's 23–69°, mostly 25–55°. (See Fig. 5.)

Dimensions: In specimens examined: From Oslo Fiord: girdle diameter 48–63 μ , mostly 54–63 μ ; length hypotheca 30–42 μ ; length epitheca 24–33 μ ; angle made by intersection of projections of base of hypotheca and girdle 23–35°; length apical horn 168–294 μ . From NIOE station 121: girdle diameter 48–54 μ ; length hypotheca 27–33 μ ; length epitheca 18–27 μ ; angle between hypotheca base and girdle 25–33°; length apical horn 228–300 μ . From Agulhas current NGY stations: girdle diameter 42–51 μ , mostly 42–48 μ ; length hypotheca 24–30 μ ; length epitheca 15–24 μ ; angle between base of hypotheca and girdle 21–35°; length apical horn 138–525 μ . *From literature: Girdle diameter:* cold water forms 48–57 μ , warm water forms, including Mediterranean 45–55 μ , exceptionally up to 70 μ , (Jørgensen 1911); from Mediterranean, 58, 65 μ (Paulsen 1930); from off Vigo, Spanish Atlantic coast, 45–70 μ (Margalef & Duran 1953); S. Pacific 42–55 μ (Steemann Nielsen 1934); off San Diego 50–60 μ (Kofoid 1907b); Mutsu Bay, Japan 50–68 μ (Abé 1927); Gulf of Pê Hai (Gulf of Chili), China 43–48 μ (Wang 1936); Indian ocean, localities unknown, 65–68 μ (Karsten 1907)*, 88 μ (Karsten 1907, Pl. 49, Fig. 27c)*; Shetland Isles 68 μ (Vanhoeffen 1897)* off

* Estimated from scale of figures.



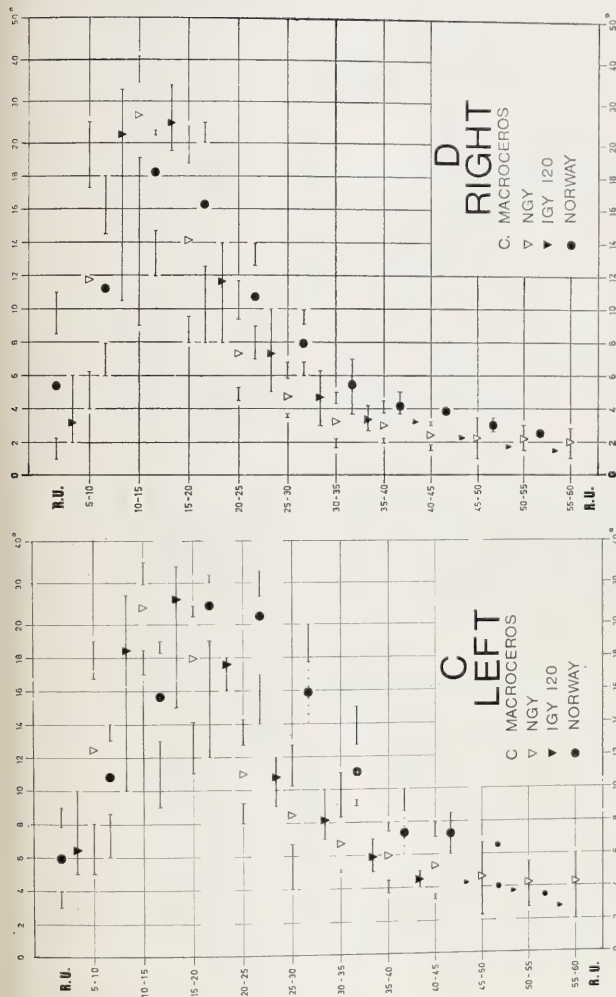


FIG. 5A-D.

C. macroceros (Ehb.) Vanh.: Antapical horn curvature in specimens from Oslo Fiord Norway, S.W. Indian ocean station NIOE 121, and Agulhas current NGY stations. A, curvature of left horn expressed in polar co-ordinates, that is, in degrees at intervals of 5 R.U. from 5 to 50 R.U., and at intervals of 10 R.U. from 50 to 100 R.U., (R.U. = radius unit, one radius unit is approximately equal to 3μ); the symbols represent the mean degree co-ordinate value at successive 5 or 10 R.U. intervals for all specimens examined, the space between the thick transverse lines and the symbols indicates the Standard Deviation for each set of measurements, and the thick transverse lines indicate the range of measurements recorded beyond the limits of the S.D., or, where the S.D. was not calculated, the range of measurements recorded; where no measurements are recorded beyond the S.D., the S.D. is indicated by a dotted line; B, the same for the right horn; C, the rate of change of direction of curvature of the left horn, expressed in degrees over 5 R.U., from 5-10 to 55-60 R.U.; the symbols represent the mean rate of change in degrees over 5 R.U. for all specimens examined; D, the same for the right horn. The small symbols and V's represent single specimens.

Greenland 57 μ (Graham & Bronikowsky 1944)*. Length apical horn 270–400 μ (Jørgensen 1911).

The foregoing measurements do not apply to heteromorphic cells apparently belonging to this species, nor specimens referred to as '*C. californiense*' Kof.

THE PROBLEM OF '*C. californiense*' KOF. AND HETEROMORPHIC FORMS OF SECTION

MACROCERAS

The occurrence of heteromorphic cells in *Ceratium* has been mentioned (Reinecke 1971). In Section *Macroceras* there appear to be four records of heteromorphic cells which may be identified with certainty as belonging to specific taxa.

In the first case, small heteromorphic cells appeared in a single cell culture of normal vegetative *C. tenue*† (Von Stosch 1964). The heteromorph was about one third of the girdle diameter of the normal vegetative cell, with a short apical horn, its length not much longer than that of the body, and straight, backwardly directed, short antapical horns, shorter than the girdle diameter, with closed rounded-tapered tips. In one instance a heteromorph was observed to undergo what appeared to be conjugation with a larger cell of normal vegetative appearance.

The second case (Steidinger & Williams 1970, Figs. 36c, d) is a record of a specimen (l.c. Fig. 36c) described as a "daughter cell" of a normal *C. trichoceros* cell (l.c. Fig. 36d). The heteromorph is 35 μ in diameter, with a long apical horn, about three times the length of the body, with antapical horns similar to those of the *C. tenue* heteromorph, and the right side of the body straight, almost truncated, in appearance.

The remaining two cases are two figures of two-celled chains of *C. macroceros*, (Jørgensen 1911, Fig. 6, from near Bergen, and Peters, fide Schiller 1937, Fig. 468b, locality not given). The anterior cell is the heteromorph, the posterior cell a typical vegetative cell. In all cells, the girdles are fully formed and the diameter of both cells in each chain is the same. Apparently, following the division of a normal vegetative cell, the parental anterior half has produced a daughter posterior half with short, backwardly directed straight horns in Jørgensen's specimen, and slightly longer, backwardly directed, but divergent, horns in that of Peters. In the heteromorphs, the tips of the antapical horns are tapered, almost pointed and closed, and in Jørgensen's specimen, the right side of the body is straight. The question of the nature of these heteromorphs is unsolved. Do the antapical horns continue growing, and eventually recurve forwards as is the case in typical members of Section *Macroceras*?

* Estimated from scale of figures.

† Referred to as *C. horridum* (Cl.) Gran by Reinecke (1971).

If the antapical horns of the anterior cell in Peters' chain were to continue growing and eventually recurve forwards, the ratio $\frac{L_{90}}{D}$ would be greater than that recorded for normal vegetative *C. macroceros* cells. Schiller (l.c. Fig. 468c) gives a second figure of Peters of a solitary heteromorph, with longer antapical horns with closed pointed ends, which are divergent and slightly curved, but show no recurvature forwards. Jörgensen (1911 Fig. 136) depicts a solitary heteromorph, from the Gibralter Straits, with similar slightly shorter antapical horns, the left one showing the beginning of a forward recurvature, which would give an estimated $\frac{L_{90}}{D}$ of about 2.73. Halim (1963) figures in which a specimen both antapical horns have a forward recurvature, the left horn extending to just beyond the 90° co-ordinate, the right to just beyond the point of MBC; the horn tips are pointed and closed, the ratio $\frac{L_{90}}{D}$ is about 2.00, the right horn MBC radius co-ordinate is about twice that of the left horn and the right side of the body is truncated.

Kofoed (1907b) published a new species *C. californiense* from off San Diego, illustrating three specimens, with complete girdles. In the first, (l.c. Pl. 23, Figs. 8,9), the apical horns are long, the right side of the body is truncated, the girdle diameter is about 35 μ , the antapical horns show a forward recurvature which does not reach the 90° co-ordinate, and the tips of the antapical horns are pointed and closed. A difference in thickness of the thecal wall at the base of all three horns indicated, according to Kofoed (1908a): "proximal growth . . . without preceding autotomy". The two other specimens (l.c. Figs. 6,7) have a diameter of about 45 μ short apical horns, a rounded right body profile, and short antapical horns with closed tapered tips, not exceeding the length of the girdle diameter, which are divergent and curve slightly. Whether or not all four specimens belong to the same species is debatable.

Pavillard (1931) depicted a specimen from off Portugal, which he named *C. californiense*, in which the girdle is apparently complete, the girdle diameter about 43 μ , the MBC radius co-ordinates long relative to the girdle diameter, the antapical horns are recurved forwards to a level beyond the top of the epitheca and are shown with truncated open ends, and the ratio $\frac{L_{90}}{D}$ is about 2.33. A similar specimen from off Monaco is figured by Jörgensen (1911), but the antapical horns are shown, with open truncate tips, extending to about the point of MBC. Jörgensen considered *C. californiense* to be the front cell of a heteromorphic chain of *C. macroceros*, as all the heteromorphs he examined had newly formed posterior halves, which he termed "f. postico-juvenile", and named them "*C. gallicum* f. *californiense*" in the key to the figures. Pavillard, however, wrote of *C. californiense*: "constitue sûrement une espèce autonome (contra Jörgensen)."

Karsten (1907, Pl. 51, Fig. 15, under the name *C. californiense*, girdle diameter estimated at 52 μ) and Jörgensen (1920, Fig. 80, under the name *C. macroceros*

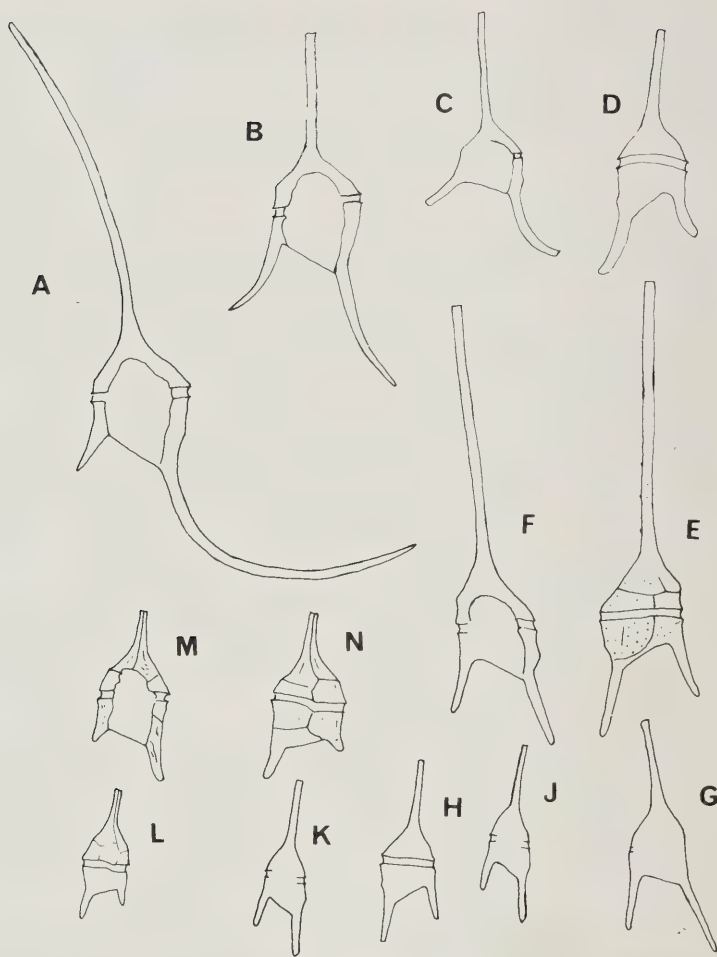


FIG. 6.

Heteromorphs of species of *Ceratium* found in samples from the Port Elizabeth line of NGY Agulhas current stations, (12 heteromorphs in 3 200 ceratium cells examined). Girdle diameters: A 45 μ , B 45 μ , C 33 μ , D 36 μ , E 39 μ , F 37 μ , G 27 μ , H 28 μ , J 23 μ , K 23 μ , L 23 μ , M 33 μ . A and B resemble to some extent, specimens referred to as '*C. macroceros*' or '*C. gallicum f. californiense*' by Schiller (1937) and Jørgensen (1911); C could be an unusually small form of *C. macroceros*; E and F, particularly E, resemble the heteromorph of *C. trichoceros* pictured by Steidinger & Williams (1970); G and H resemble to some extent the putative male gamete observed in a culture of *C. tenue* by Von Stosch (1964); M and N are ventral and dorsal views of the same specimen.

subsp. gallicum f. californiense, diameter estimated at $57\ \mu$, and Fig. 92, under the name "*C. (horridum subsp.) buceros* Zach. a degenerate form answering to *f. californiense* (Kof.) of *C. macroceros subsp. gallicum*", diameter unknown) published figures of specimens with short slightly curved antapical horns similar to Kofoid's Figs. 6 and 7. In Jörgensen's specimens, the right profile of the body is truncated. For some unstated reason, Jörgensen considered Karsten's figure to belong to *C. deflexum*. The small spines along the lower edges of the antapical horns are, however, not typical of *C. deflexum*.

In the Agulhas current samples, a number of heteromorphs were seen, some of which resembled the small heteromorph of *C. tenue* recorded by Von Stosch, others the heteromorph of *C. trichoceros* photographed by Steidinger & Williams, one which resembled Jörgensen's Fig. 80, with a girdle diameter of $45\ \mu$, and one in which the right horn was very short and the left horn was longer and recurved forwards to just beyond the 90° co-ordinate. In the latter, the diameter is $45\ \mu$, the right side of the body truncated, the tips of the antapical horns pointed and closed, the ratios $\frac{L_{90}}{D}$ 2.02 and $\frac{B}{H}$ 1.78 and the left horn MRC 8° , all outside the range of polar co-ordinate measurements recorded for specimens of *C. macroceros* from this area. This specimen cannot be regarded as belonging to *C. trichoceros* because the left horn MRC occurs between the 60 and $90\ \mu$ radius co-ordinates (over two successive $15\ \mu$ intervals) and the left horn MBC degree co-ordinate is 62° . (See Fig. 6.)

At this stage it is quite impossible to classify these heteromorphs unless they arise in single cell cultures of normal vegetative cells or are associated in chains with normal cells. Circumstantial evidence certainly suggests that for some reason, normal *C. macroceros* cells sometimes divide into two cells, of which the one with the parental anterior half produces a new posterior half with antapical horns, which, if fully developed, have for the size of the cell, somewhat longer MBC radius co-ordinates and a higher ratio $\frac{L_{90}}{D}$ (> 2.00) than normally found; the antapical horns are, however, often seen as short, straight and backwardly directed, or only slightly curved, with closed pointed tips.

Experiments to determine conditions under which heteromorphs are formed, their variation and whether or not they are involved in sexual reproduction would be very desirable.

It is of interest to note that Jörgensen (1920) found the heteromorph of Fig. 80 in the Sea of Marmora, apparently associated with conditions of low salinity.

Ceratium deflexum (Kofoid) Jörgensen (1911): 64, Pl. 7, Fig. 138.

Diagnosis: *C. deflexum* generally differs from all other taxa in this Subsection in exhibiting a ventral deflection of the antapical horns. In terms of polar co-ordinate measurements of two dimensional camera lucida drawings of the

specimens examined, *C. deflexum f. deflexum* and *C. deflexum f. deflectomassum* Rein. differ from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75μ radius co-ordinate; *C. deflexum f. sinensis* Rein. differs from *C. trichoceros* in that the right horn MBC degree co-ordinate is $\leq 40^\circ$.

C. deflexum differs from *C. massiliense* (Gour.) Kars. in that the sum of the left and right horn MRC's is $\geq 40^\circ$; (*f. deflexum* and *f. deflectomassum* differ from the single specimen of *C. massiliense var. carriense* (Gour.) Rein. recorded in which the sum of left and right horn MRC's is $> 40^\circ$ (Jørgensen (1911) Fig. 150a) in that the left horn degree co-ordinate with the 150μ radius co-ordinate is $> 135^\circ$; *f. sinensis* differs from this specimen in that the right horn MBC radius co-ordinate is $> 60 \mu$).

F. deflexum differs from a number of specimens of *C. macroceros* (Ehb.) Vanh. in that the left horn MRC occurs before the 75μ radius co-ordinate; *f. deflexum* differs from those specimens of *C. macroceros* in which the left horn MRC occurs before the 75μ radius co-ordinate in that the left horn degree co-ordinate with the 105μ radius co-ordinate is generally $\geq 150^\circ$; (*f. deflexum* differs from the single specimen of *C. macroceros* in which this co-ordinate was 152° in that the difference between left and right horn MBC degree co-ordinates is $> 15^\circ$); specimens of *f. deflexum* in which the left horn degree co-ordinate with the 105μ radius co-ordinate is $< 150^\circ$, differ from *C. macroceros* in that the difference between left and right horn MBC degree co-ordinates is $> 20^\circ$ and/or the right horn degree co-ordinate with the 105μ radius co-ordinate is $> 115^\circ$; (*f. deflexum* differs from the two specimens of *C. macroceros* in which the difference between left and right horn MBC degree co-ordinates was $> 20^\circ$, in that the degree co-ordinate with the 105μ radius co-ordinate is $> 135^\circ$ in the left horn and $> 100^\circ$ in the right). *F. deflectomassum* differs from *C. macroceros* in that the ratio $\frac{L_{90}}{D}$ is < 0.90 , the left horn degree co-ordinate with the 105μ radius co-ordinate is $> 135^\circ$, the difference between left and right horn MBC degree co-ordinates is $> 20^\circ$ and the ratio $\frac{B}{H}$ is generally < 0.90 . *F. sinensis* differs from *C. macroceros* in that the difference between left and right horn MBC degree co-ordinates is $> 20^\circ$ and the sum of left and right horn MRC's is $> 45^\circ$ and the right horn MBC radius co-ordinate is $> 60 \mu$. *C. deflexum* differs further from *C. macroceros* in that the antapical horns are never ornamented with prominent spines and lists and the girdle is always fully developed.

C. deflexum differs from *C. tenue* O. & S. in that the right horn degree co-ordinate with the 15μ radius co-ordinate is $< 40^\circ$.

Ventral deflection of antapical horns: The character used by Kofoid to distinguish his new taxon was the "marked" ventral deflection of the antapical horns. As the antapical horns leave the body, they are directed posteriorly and ventrally,

so that the recurved distal parts do not lie in the same plane as the body and apical horn. Kofoed found this deflection sometimes in excess of one girdle diameter.

In the Agulhas current NGY specimens it was variable, and sometimes not very marked, when the specimens could have been confused with *C. massiliense* var. *massiliense* or *C. macroceros* in its cold water form. Indeed, Karsten (1907) included specimens of all three taxa under the name *C. tripos macroceras*. Jørgensen (1911) commented that *C. deflexum* was often confused with *C. macroceros*, but Graham & Bronikowsky (1944) wrote that, once seen, *C. deflexum* was easily recognised.

The ventral deflection of the antapical horns is difficult to measure accurately under the microscope with a graduated fine adjustment screw, because of backlash. It was investigated in 13 NGY specimens, by measuring the difference recorded on the fine adjustment screw when first focussing on the base of the apical horn and then on portions of the antapical horns at the same level, when the specimen was seen in full dorsal or ventral view. Differences recorded varied from 5 to 50 units, and the ventral deflection was roughly the same for left and right horns.

Discussion of some specimens in the literature: *C. deflexum* was originally described as a subspecies of *C. macroceros*, when 'subsp. *macroceros*' was generally regarded as a cold water taxon. There are illustrated records of specimens named *C. macroceros* from South of latitude 30° N., which, from their antapical horn polar co-ordinate measurements, resemble *C. deflexum* rather than *C. macroceros*, but obviously do not have a marked ventral deflection of the antapical horns. They are those of Ostenfeld & Schmidt (1901) from the Red Sea and Gulf of Aden and Klement (1964) from the Gulf of California. They are treated here as specimens of *C. deflexum*.

Peters (1932) investigating the ceratia of the S. Atlantic, incorporated *C. deflexum* in *C. massiliense* because of the presence of many transitional forms, but published no figures or descriptions. Graham & Bronikowsky, after studying the ceratia of the N. Atlantic, concluded that Peters had been dealing with *C. deflexum*-like variants of *C. massiliense*. The specimen they illustrate (l.c. Fig. 22H) is regarded here as belonging to *C. deflexum* f. *deflectomassum*.

The problem taxon *C. macroceros* var. *hainanensis* Nie (1936) is now discussed. It was cited by Sournia (1967) as a synonym of '*C. macroceros* var. *macroceros*'. It was described from Hainan, where individuals were frequently observed from Shin-tuen. Nie made no comment on any ventral deflection of the antapical horns, describing the thecal walls as less robust than in the type, with a list generally present in the angle between the base of the hypotheca and left horn; the girdle is completely formed, girdle diameter is 64–70 μ and the

antapical horns are depicted as smooth. Nie also recorded *C. deflexum*, describing the ventral deflection of the antapical horns as "marked" and giving a girdle diameter of 57–62 μ . The antapical horn polar co-ordinates of Nie's figures of *var. hainanensis* resemble those of figures of some specimens described by Böhm (1931b) as *C. deflexum*. Working on samples from the S.W. Monsoon current, Böhm found *C. deflexum* in stations just to the West and South of Hainan. He observed two forms, one with a diameter of 50–60 μ and short MBC radius co-ordinates, with the left horn MRC occurring before the 75 μ radius co-ordinate, the other with a diameter of 60–68 μ , longer MBC radius co-ordinates and the left horn MRC generally occurring beyond the 75 μ radius co-ordinate. Böhm made no comment on ventral deflection of the antapical horns. In the same area, he found *C. macroceros* to be "rather uncommon as *subsp. gallicum*" in samples from South of 20°N. It is the large forms of *C. deflexum* depicted by Böhm which *var. hainanensis* resembles. The latter is also similar to specimens illustrated by Karsten, (1907, Pl. 51, Fig. 11a, b, classified by Jörgensen (1911) as *C. deflexum*), from an unnamed locality, presumably a station in the East Indies, under the name *C. triplos macroceras*.

C. deflexum is also recorded from the S. China Sea by Steemann Nielsen (1939) and appears to have been illustrated by Okamura (1907) from off the coast of Japan as "*C. macroceras* f.?" for the figure shows what looks like antapical horn deflection (l.c. Fig. 20a).

The East coast of China and Indo China is affected by the warm S.W. monsoon current in summer and the cold N.E. monsoon current in winter, which could cause a variation in the appearance of specimens of *C. macroceros* in the area, but none of the figures of *C. macroceros* from these waters depicted in the literature resembles Nie's figures of *var. hainanensis*. Accordingly, it is treated provisionally as belonging to *C. deflexum*, representing specimens in which the ventral deflection of the antapical horns is not very marked.

General description: Horn disposition and length: Antapical horns slightly to markedly ventrally deflected; initially both horns directed backwards and then recurved anteriorly, usually fairly abruptly; distal parts lie parallel to, to somewhat diverging from, the apical horn, not in the same plane as it or the body; base of left horn makes an indistinct to an obvious angle with base of hypotheca. Antapical horns often found broken (or autotomised?) at level of mid apical horn length, or with closed rounded tips extending to level of two thirds of apical horn length; (Nie, 1936, depicts a specimen in which antapical horns are long, the distal parts slightly undulating, and extend beyond a shortish apical horn). Length of apical horn in NGY specimens: 177–420 μ (in one case 60 μ , could have been broken); from literature: 210–425 μ (Jörgensen 1911), 100–450 μ (Nie 1936). *Thecal ornamentation:* Girdle always fully developed; thecal wall

generally unmarked, very occasionally thickened with slight ridges; apart from left sulcal list, list usually present in angle between base of left horn and hypotheca, extending along hypotheca base for up to two thirds of length of base; list margin usually smooth, rarely unevenly serrated; occasionally a third narrow list present along base of sulcus; apical horn smooth; antapical horns smooth or, rarely, with minute spines along lower edges in region of recurvature, which may support an insignificant list. (See Figs. 7, 8.)

Distribution: The distribution of *f. deflexum* and *f. deflectomassum* at the NGY Agulhas current stations is shown in Tables 1 and 2.

Sournia (1967) suggested that the records of *C. deflexum* were sparse because of its confusion with *C. macroceros*. Nielsen (1934) described *C. deflexum* (*sensu stricto*) in the S. Pacific as a typical surface species, from oceanic and neritic waters, rare in truly oceanic waters, and in the Indian Ocean (1939), as very frequent in both neritic and oceanic waters. Graham & Bronikowsky (1944) said it was an intolerant, (closely restricted to regions with surface temperatures of 19°C or more), tropical surface species, with an apparent preference for eutrophic water, for in the Carnegie Pacific samples, the greatest numbers were recorded from stations where the phosphate content was above 25 mg. PO₄/m³.

F. deflexum appears to be confined to the Pacific and Indian oceans; *f. deflectomassum* is recorded from all oceans and *f. sinensis* has to date only been recorded from the Indian ocean, probably in the vicinity of the East Indies, (the exact locality of Karsten's specimens is uncertain), and the S. China Sea.

Records of any forms of *C. deflexum* from the Mediterranean are not proven. It was not recorded by Jörgensen (1920) and there are only two unillustrated records: Pavillard (1937: 9) listed *C. deflexum* in phytoplankton records for the Monaco Sea, but wrote "identifications doubtful"; Travers & Travers (1962: 57) recorded a single specimen from the Gulf of Marseille, noting "semblait bien caractérisé et différent de *Ceratium macroceros*". Likewise, the presence of *f. deflexum* in the Atlantic is doubtful. Apart from Graham & Bronikowsky's figure of *f. deflectomassum* no other figures of *C. deflexum*-like specimens from the Atlantic have been published.

Ceratium deflexum f. deflexum

C. deflexum (Kofoid) Jörgensen (1911): 64, Pl. 7, Fig. 138; Böhm (1931b): 37, e.p., Fig. 33a-d, non e-g, nec Fig. 34 (= *f. sinensis*); Steemann Nielsen (1934): 25, Fig. 63; (1939): 14; Nie (1936): 63, Fig. 29 A, B; Schiller (1937): 428, Fig. 467a (= Böhm Fig. 33a), non b (= *C. recurvatum* Schröder 1906 Fig. 40); Graham & Bronikowsky (1944): 39, Fig. 22 C, D; Wood (1954): 310, Fig. 237; Sournia (1967): 463, Fig. 86.

"*C. macroceros deflexum* subsp. nov." Kofoid (1907b): 304, Pl. 24, Figs. 13-15.

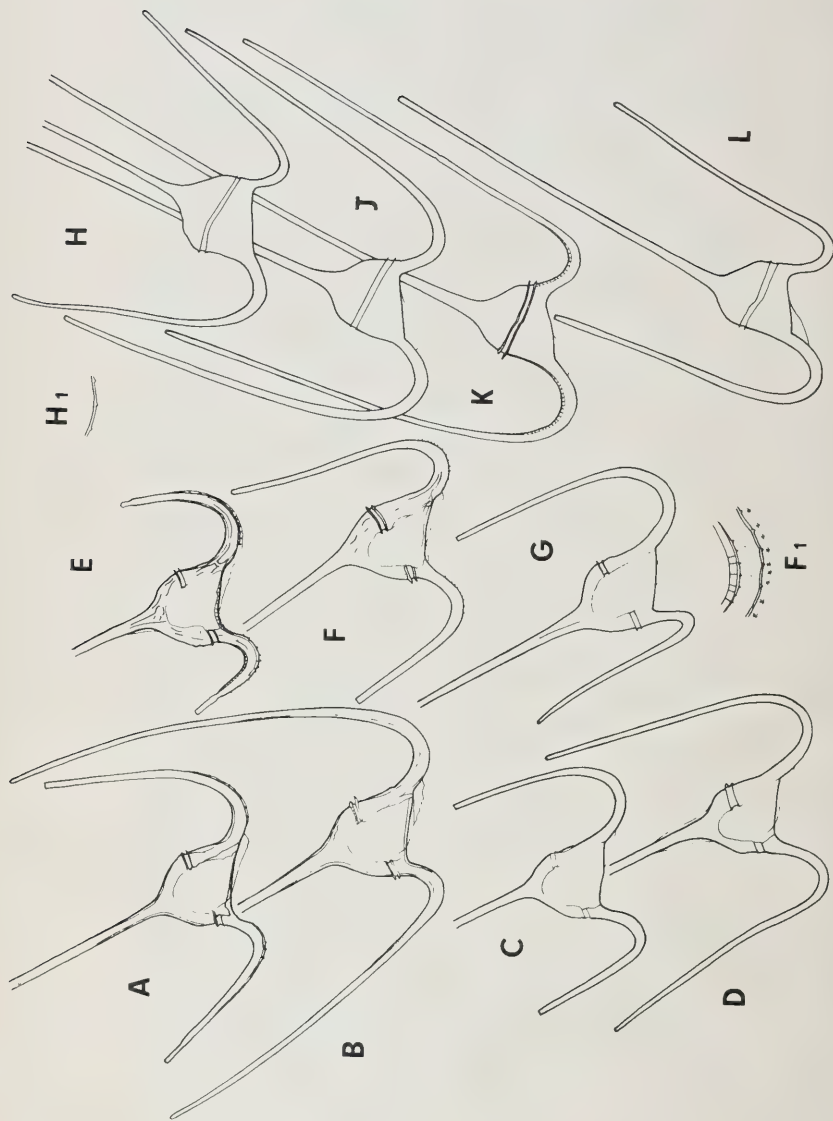


Fig. 7.
C. deflexum (Kof.) Jörg.: All specimens from Agulhas current NGY samples, except F; the measurements given for each figure are, in order, the girdle diameter, the sum of left and right horn MRC's and in some cases, the ventral deflection of the antapical horns, (see page 304).
 A, *f. deflectionum* Rein., 60 μ , 49°; 5 units; B, *f. deflexum*: B, specimen from NGY 42, thecal wall in optical section and surface view, 66 μ , 80°; 30 units; C, 54 μ , 81°; 45 units in left horn, 1 in right; D, 57 μ , 94°; 45 units in left horn, 1 in right; E, from NGY 41 (see page 71), thecal wall in optical section, 66 μ , 80°; 30 units; F, regeneration of tips of antapical horns, 63 μ , 62°; 29 units in left horn, 1 in right; G, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; H, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; I, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; J, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; K, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; L, from S. Indian Ocean station N 08 E 121, 66 μ , 65°, 44 units in left horn, 1 in right; F1, detail of lower edge of left horn, 57 μ , 58°, 15 units; K, thecal wall in optical section, 60 μ , 52°, 29 units; L, 54 μ , 103°.

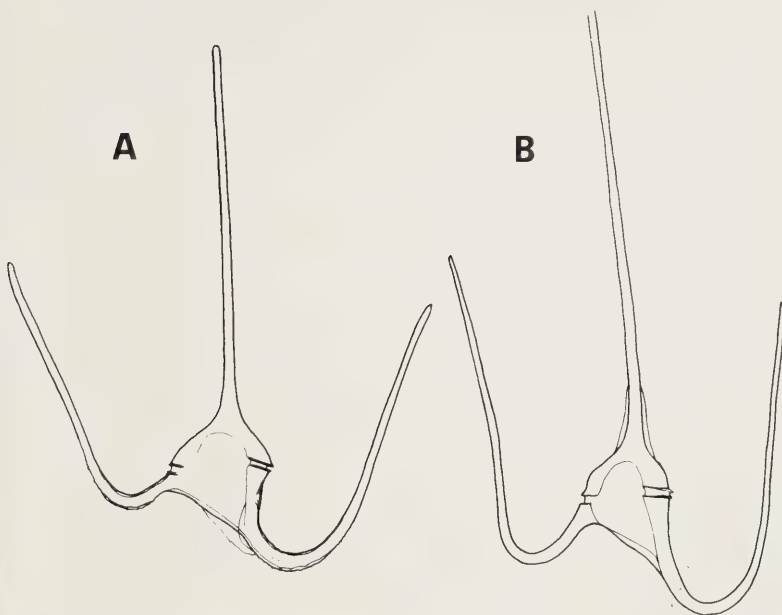


FIG. 8.

C. deflexum (Kof.) Jörg.: Specimens from Agulhas current NGY samples. **A**, *f. deflectomassum* Rein., 60 μ , 49°, 7–10 units; **B**, *f. deflexum*, 57 μ , 94°, 31 units. (See Key to Fig. 7.)

"*C. macroceras* Ehb., f?" Okamura (1907): 128, Pl. 4, Fig. 20a, b non *C. macroceras* (Ehb.) Vanh.

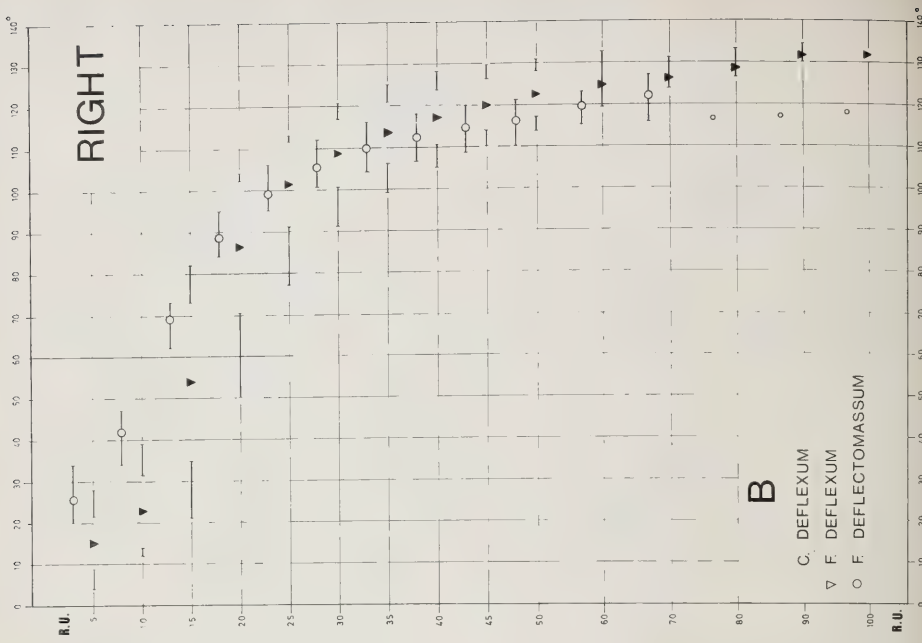
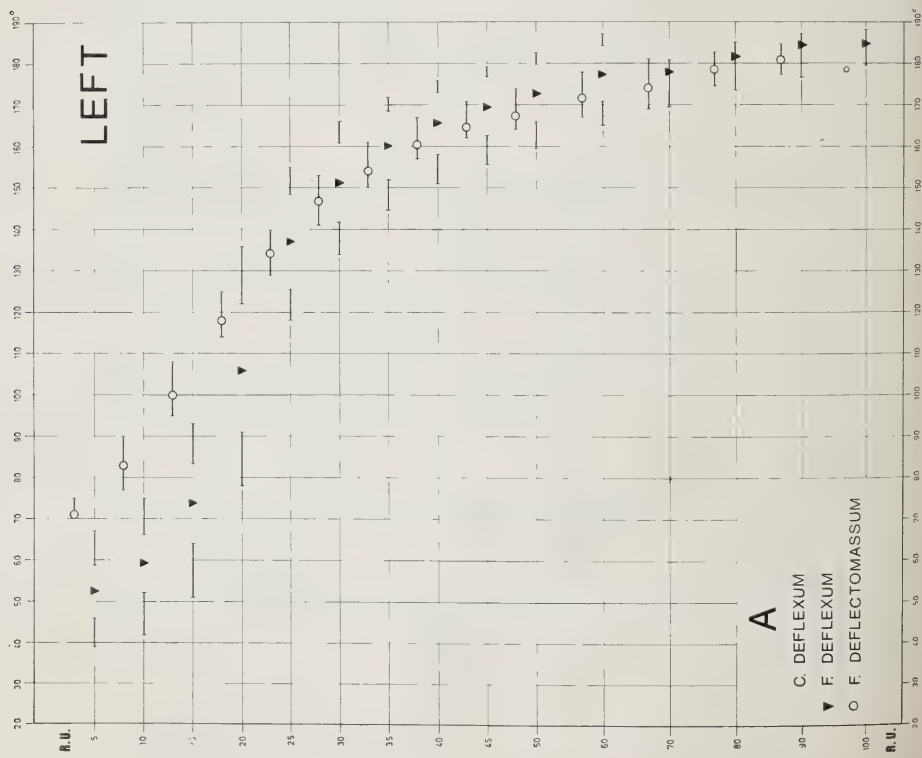
"*C. macroceras* (Ehb.)" Ostenfeld & Schmidt (1901): 167, Fig. 19.

"*C. tripos macroceras*" Karsten (1907) e.p., Pl. 49, Fig. 26a, non b (= *f. sinensis*).

"*C. tripos robustum* Ost. & Schm. var." Karsten (1907): 413, e.p., Pl. 51, Fig. 7, non Pl. 48, Fig. 13a, b (= *C. vultur* Cl.), non *C. robustum* O. & S. (1901) (= *C. vultur*).

Diagnosis: Differs from *f. deflectomassum* in that the sum of the right and left horn MRC'S is $> 50^\circ$; differs from *f. sinensis* in that the right horn MBC radius co-ordinate is $< 55 \mu$.

Description: Antapical horns usually markedly ventrally deflected. Horn curvature expressed in polar co-ordinate measurements of two-dimensional camera lucida drawings: *Left horn* MBC co-ordinates $51\text{--}78^\circ$ and $15\text{--}48 \mu$, mostly



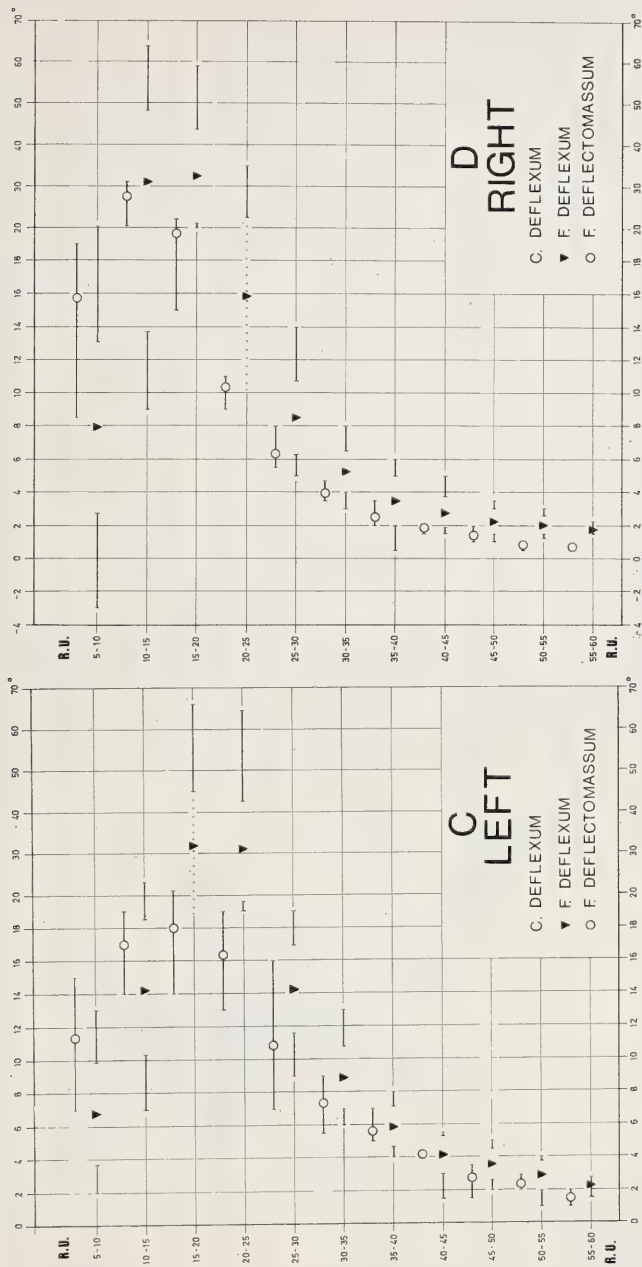
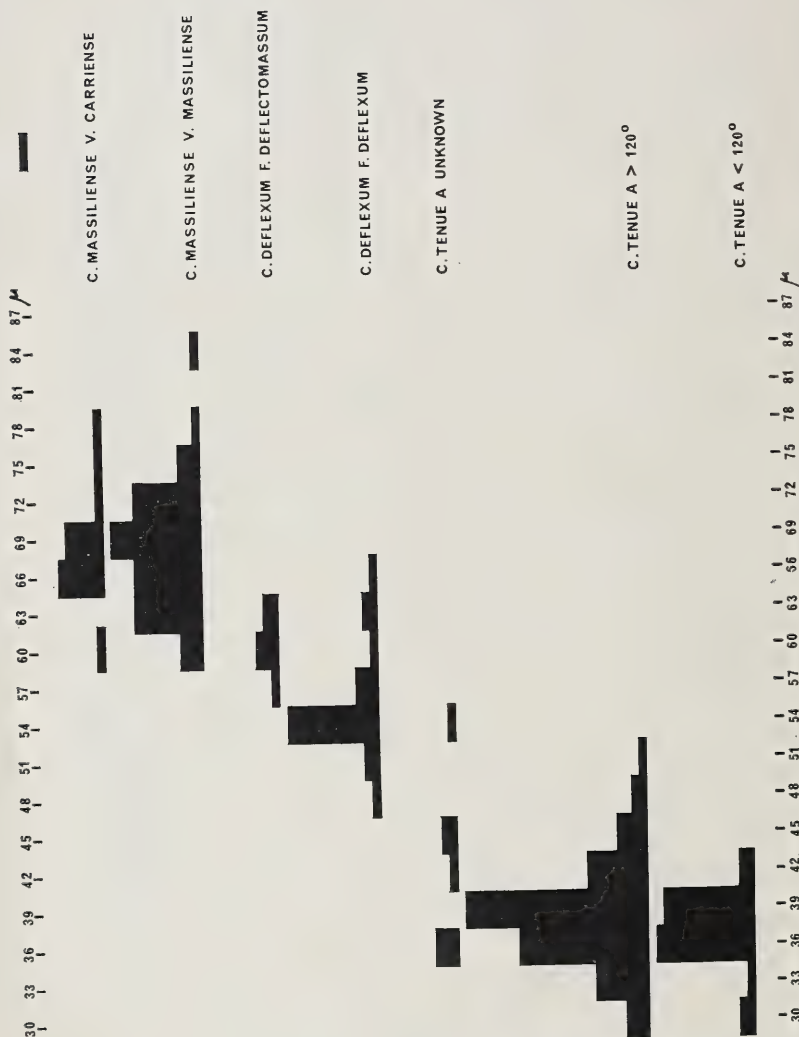


FIG. 9A-D. *C. deflexum* (Kof.) Jörg.: Antapical horn curvature in specimens from Agulhas current NGY stations. A, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at intervals of 10 R.U. from 50 to 100 R.U.; B, the same for the right horn; C, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U., from 5-10 to 55-60 R.U.; D, the same for the right horn. See Key to Fig. 5.



Variation in girdle diameter in specimens of *C. massiliense* (Gour.) Kar., *C. deflexum* (Kof.) Jörg. and *C. tenue* O. & S. from NGY Agulhas current samples. (The single bar indicates one specimen; A = right horn degree co-ordinate with 150 μ radius co-ordinate.)

58–68° and 31–40 μ in NGY specimens; degree co-ordinate with 15 μ radius co-ordinate 39–78°, mostly 46–58° in NGY specimens; with 105 μ , 145–179°, (138° in a single case), mostly 152–169° in NGY specimens; with 150 μ , generally exceeding 160°; MRC occurs between 45 and 75 μ radius co-ordinates, very rarely between 30 and 45 μ , and is 21–66°, mostly 26–51° in NGY specimens; $\frac{L_{90}}{D}$ 0,48–1,18, mostly 0,85–1,07 in NGY specimens; $\frac{B}{H}$ 0,42–1,18, mostly 0,66–0,96 in NGY specimens. *Right horn*: MBC degree co-ordinate 26–48°, mostly 32–43° in NGY specimens, less than in left horn by 14–38°, mostly by 20–33° in NGY specimens; MBC radius co-ordinate 25–53 μ , mostly 34–47 μ in NGY specimens, very slightly less than, to up to 20 μ greater than in left horn, 2–7 μ greater than in left horn in most NGY specimens; degree co-ordinate with 15 μ radius co-ordinate 4–28° mostly 8–22°, in NGY specimens, less than in left horn by 18–56°, mostly by 27–48° in NGY specimens; degree co-ordinate with 105 μ radius co-ordinate 93–129°, mostly 106–121° in NGY specimens; MRC generally occurs between 30 and 60 μ radius co-ordinates, very rarely between 15 and 30 μ or 60 and 75 μ , and is 23–64°, mostly 31–55° in NGY specimens; $\frac{R_{90}}{D}$ 0,76–1,91, mostly 0,90–1,30 in NGY specimens. Sum of left and right horn MRC's 51–113°, mostly 64–101° in NGY specimens. (See Fig. 9.)

Dimensions: In NGY specimens: Girdle diameter 48–66 μ , mostly 54–57 μ ; length hypotheca 27–42 μ ; length epitheca 24–33 μ ; angle between base of hypotheca and girdle 23–36°. (See Fig. 10.) *From literature*: Girdle diameter 54–64 μ (Jørgensen 1911), 50–60 μ (Böhm 1931b), 57–62 μ (Nie 1936).

***Ceratium deflexum* f. *sinensis* Reinecke forma nova.**

C. deflexum: Böhm (1931b): 37, e.p., Figs. 33e–g, 34a, b *non* 33a–d (= *f. deflexum*).

“*C. tripos macroceras*” Karsten (1907) e.p., Pl. 49, Fig. 26a *non* b (= *f. deflexum*), Pl. 51, Fig. 11a, b.

? *C. macroceros* var. *hainanensis* Nie (1936): 62, Fig. 28A, B.

Diagnosis: Differt a *f. deflexo* et *f. deflectomasso* in eo quod co-ordinatus radii cornus dextri apud locum flexus maximi retrorsum $\geq 60 \mu$ est, et cursus mutationis maximi flexus per 15 μ cornus sinistri plerumque extra co-ordinatum radii 75 μ accidit.

Diagnosis: Differs from *f. deflexum* and *f. deflectomassum* in that the right horn radius co-ordinate at the point of maximum backward curvature is $\geq 60 \mu$, and the maximum rate of change of direction of curvature over 15 μ generally occurs beyond the 75 μ radius co-ordinate in the left horn.

Description: Ventral deflection of antapical horns sometimes not very marked. Polar co-ordinate measurements of horn curvature in camera lucida drawings

from the literature generally as in *f. deflexum*, with the following differences: MBC radius co-ordinates sometimes larger in left horn and always larger in right horn, being 60–78 μ ; MBC degree co-ordinate generally smaller in right horn, being 14–33° (40° in one case); difference between left and right horn MBC degree co-ordinates never < 20°, being 26–49°; degree co-ordinate with 105 μ radius co-ordinate often lower in both left and right horns; left horn MRC generally occurs beyond 75 μ radius co-ordinate; sum of left and right horn MRC's sometimes as low as 46°; $\frac{L_{90}}{D}$ 0,86–1,57; $\frac{R_{90}}{D}$ 1,63–2,62; $\frac{B}{H}$ 0,90–1,45.

Dimensions: From literature: Girdle diameter 64–70 μ (Nie 1936), 60–68 μ (Böhm 1931b).

Because the evidence for including *var. hainanensis* Nie in *C. deflexum* is circumstantial, the epithet "*hainanensis*" is not retained for this taxon.

C. deflexum f. deflectomassum Reinecke forma nova.

C. massiliense: Graham & Bronikowsky (1944): 38, e.p., Fig. 22H.

C. massiliense f. α macroceroides: Böhm (1931b): 35, e.p., Fig. 32b.

C. macroceros subsp. macroceros: Graham & Bronikowsky (1944): 38, e.p., Fig. 21C.

C. macroceros: Klement (1964): 357, e.p., Pl. 3, Fig. 1.

Diagnosis: Differt a *f. deflexo* in eo quod summa velocitatum maximarum mutationis flexus per 15 μ cornus dextri cornus sinistrique < 50° est; differt a *f. sinense* in eo quod co-ordinatus radii cornus dextri apud locum flexus maximi retrorsum < 55 μ est.

Diagnosis: Differs from *f. deflexum* in that the sum of the maximum rates of change of direction of curvature over 15 μ for left and right horns is $\leq$ 50°; differs from *f. sinensis* in that the right horn MBC radius co-ordinate is < 55 μ .

Description: Ventral deflection of antapical horns not very marked. Polar co-ordinate measurements of antapical horn curvature in camera lucida drawings of specimens as in *f. deflexum* save that sum of left and right horn MRC's is 40–50°, right horn MBC degree co-ordinate is never < 35°, and right horn degree co-ordinate with 105 μ radius co-ordinate may be as low as 82°. $\frac{L_{60}}{D}$ 0,50–0,88; $\frac{L_{60}}{D}$ 0,73–2,21; $\frac{B}{H}$ 0,30–0,92. (See Fig. 8.)

Dimensions: In NGY specimens: Girdle diameter 57–66 μ ; length apical horn up to 350 μ ; angle between base of hypotheca and girdle 22–33°. *From literature:* Girdle diameter 66 μ (Klement 1964).

One NGY specimen seen with closed, rounded and slightly swollen antapical horn tips.

This taxon includes specimens which are in some respects intermediate between *C. massiliense* var. *massiliense* and *C. deflexum sensu stricto*. Steemann Nielsen (1934) noted that forms of *C. massiliense* had a *C. deflexum*-like habit in some of his neritic Pacific samples, and may have been referring to the present taxon.

TAXON INCERTAE SEDIS

C. recurvatum Schröder (1906): 367, Fig. 40.

C. deflexum f. *recurvatum* (Schr.) Jörgensen (1911): 65, 123, Pl. 7, Fig. 138 (= Schröder Fig. 40).

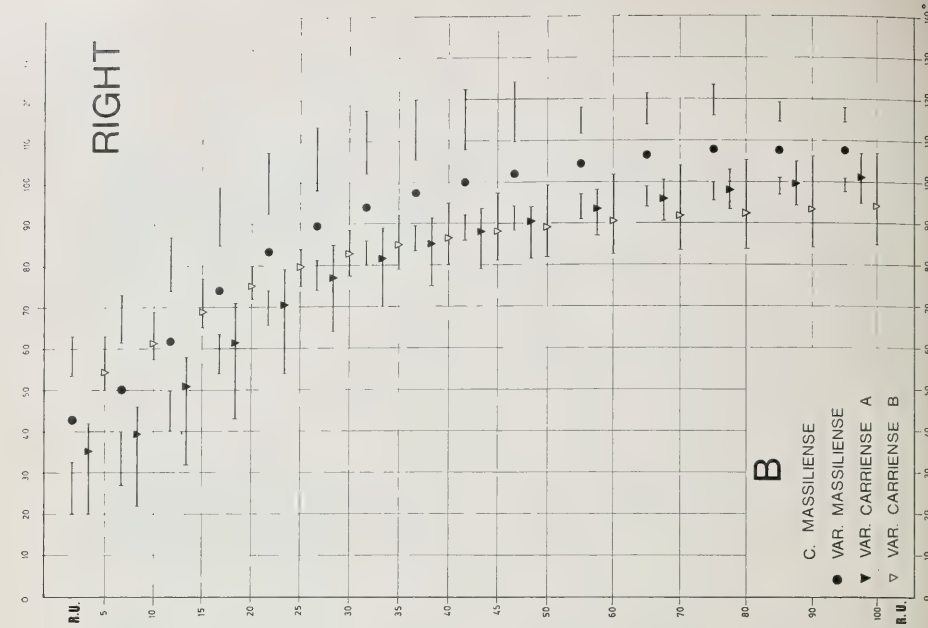
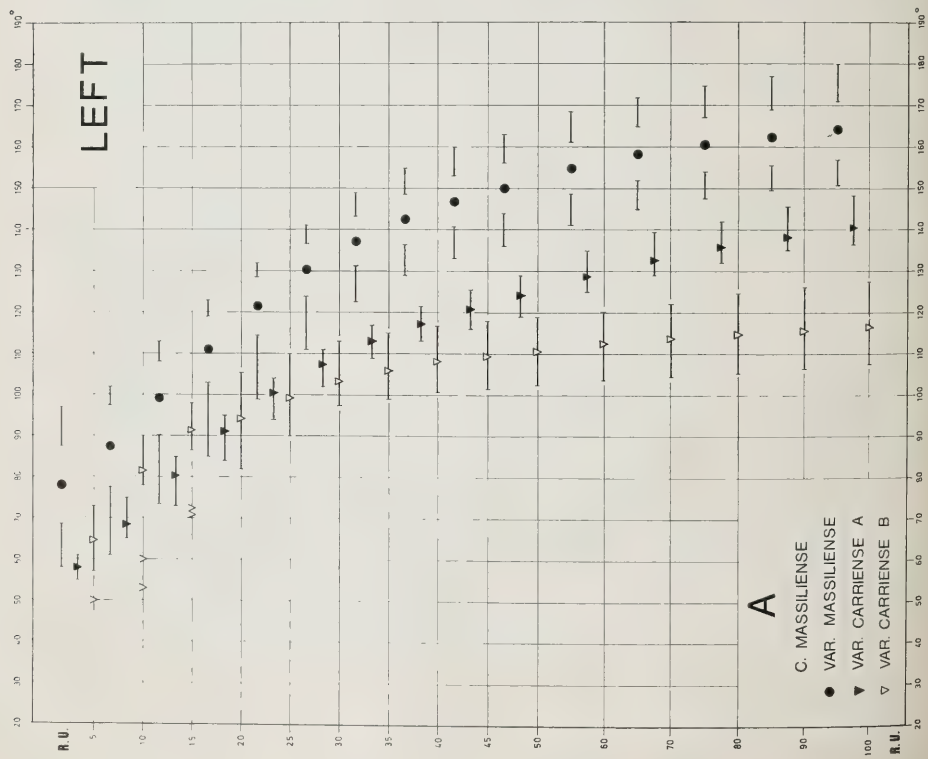
C. deflexum: Schiller (1937): 428, p.p., Fig. 467b (Schröder Fig. 40), *non a* (= *C. deflexum* f. *deflexum*).

This problematic form was found in the Arabian Sea by Schröder and later a second specimen was seen in Schröder's sample by Jörgensen (1911) who lost it before he could draw or measure it. From the scale, the diameter of Schröder's specimen is about 56 μ . If it is a freak, then it does not have taxonomic status, but, whether a freak or not, the question arises: is it related to *C. deflexum*? The shape of the body in Schröder's figure indicates that it was probably drawn seen in full ventral aspect. Polar co-ordinate measurements of the curvature of the right horn show an MRC of about 10°, which is lower than recorded in any camera lucida drawings of *C. deflexum*, while the MBC radius co-ordinate is about 75 μ .

Ceratum massiliense (Gourret) Karsten (1906): 145.

Diagnosis: In the specimens examined, *C. massiliense* var. *massiliense* and most specimens of *C. massiliense* var. *carriense* (Gour.) Rein. differ from *C. macroceros* (Ehb.) Vanh. in that the ratio $\frac{B}{H}$ is $< 0,90$; (*C. massiliense* differs from the single specimen of *C. macroceros* recorded in the Agulhas current in which this ratio was 0,83, in that the girdle diameter is $\geq 60 \mu$); the few specimens of var. *carriense* in which the ratio $\frac{B}{H}$ is $\geq 0,90$, but always $< 1,50$, differ from *C. macroceros* in that the right horn MRC is $\leq 10^\circ$ and the sum of left and right horn MRC's is $\leq 25^\circ$; (specimens of var. *carriense* in which the ratio $\frac{B}{H}$ is $\geq 0,90$, differ from the three specimens of *C. macroceros* recorded in which the right horn MRC was $\leq 10^\circ$, in that the ratio $\frac{B}{H}$ is $< 1,50$ and the sum of left and right horn MRC's is $\leq 25^\circ$ and the girdle diameter is $\geq 60 \mu$); specimens of var. *carriense* in which the ratio $\frac{B}{H}$ is $\geq 1,10$, differ further from *C. macroceros* in that the difference between the left horn radius co-ordinates of the tangent, parallel to the girdle, to the lower edge of the antapical horn and of the point of MBC, is $> 100 \mu$.

C. massiliense differs from *C. deflexum* (Kof.) Jörg. in lacking a marked ventral deflection of the antapical horns; expressed in terms of polar co-ordinate



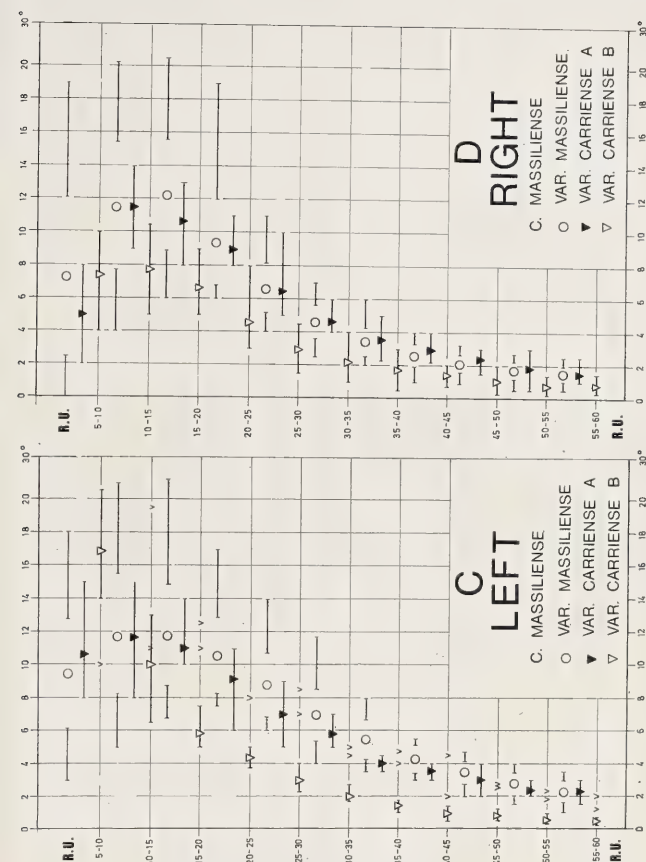


FIG. 11A-D. *C. massiliense* (Gour.) Karst.: Antapical horn curvature in specimens from Agulhas current NGY stations. A, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; B, the same for the right horn; C, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5-10 to 55-60 R.U.; D, the same for the right horn. In *var. carriense A*, the left horn degree co-ordinate with the 100 R.U. radius co-ordinate is $\geq 130^\circ$; in *var. carriense B*, this co-ordinate is $< 130^\circ$. See Key to Fig. 5.

measurements of two-dimensional camera lucida drawings, *C. massiliense* differs from *C. deflexum* in that the sum of the left and right horn MRC's is $< 40^\circ$; (a single specimen of *var. carriense*, (Jörgensen 1911, Fig. 150a), in which the sum of left and right horn MRC's was $> 40^\circ$, differed from *C. deflexum f. deflexum* and *C. deflexum f. deflectomassum* Rein. in that the left horn degree co-ordinates with the 105 and 150 μ radius co-ordinates were $< 130^\circ$, and from *C. deflexum f. sinensis* Rein. in that the right horn MBC radius co-ordinate was $< 60 \mu$).

C. massiliense differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75 μ radius co-ordinate; (the single specimens recorded of *var. massiliense* (from the Agulhas current) and of *var. carriense* (Karsten 1907, Pl. 49, fig. 27e) in which the left horn MRC occurred beyond the 75 μ radius co-ordinate, differed respectively from *C. trichoceros*, in that, in the first, the left horn degree co-ordinate with the 15 μ radius co-ordinate was $> 90^\circ$, and in the second, the girdle diameter was $> 60 \mu$ and the left horn MBC degree co-ordinate $< 70^\circ$).

C. massiliense differs from *C. tenue* O. & S. in that the girdle diameter is $\geq 60 \mu$.

Taxonomic history and present treatment of taxa: *C. massiliense*, one of the most variable species of the genus, was originally described as *C. tripos var. massiliense* by Gourret (1883: 27, Pl. 1, Figs. 2, 2a), together with *C. carriense* (l.c.: 38, Pl. 4, Fig. 57). From his drawings, it is evident that Gourret confused dorsal and ventral views and considered the apical horn to lie posteriorly. In none of the figures mentioned are lists or spines depicted. Gourret considered that the essential difference between the two taxa was that in *C. carriense*, the girdle was "concave en bas". It would appear that the specimen in Fig. 57 is drawn tilted so that the base of the hypotheca is nearest the viewer, which would account for the appearance of the girdle as "angled" in mid diameter towards the apical horn. The specimen in Fig. 2a is drawn seen slightly from one side.

In 1900, Cleve described a species, "*C. (tripos var. ?) volans*": "characterised by the straight and very long posterior horns, which proceed in a right angle to the apical horn . . . it may be possible that it is the same as *C. carriense* Gourret, which I dare not decide, without comparing the original specimens." (1900a: 15, Pl. 7, Fig. 4).

Unfortunately, in both Cleve's Fig. 4 and Gourret's Fig. 57, only the proximal parts of the antapical horns are shown, making them, together with Gourret's Fig. 2a, very unsatisfactory iconotypes. (See Fig. 16 F, G.)

The correct citation of the combination *Ceratium massiliense* has been a matter of dispute. The combination was first used by Karsten thus: "Die weiter folgenden Formen . . . gleichen am meisten dem *Ceratium massiliense* Gourret

(l.c. S. 27, Taf. 1, Fig. 2, 2a), ohne jedoch mit ihm identifiziert werden zu können." The forms he referred to were "*C. tripos protuberans* n. sp." and "*C. tripos macroceroides* n. sp.", both placed by Jörgensen (1911) in the species he then cited as "*C. massiliense* (Gourret)". Pavillard (1907) was the first to cite the species as *C. massiliense* (Gourret) Karsten applying this to Gourret's Fig. 2a, while he considered Fig. 2 to belong to "*C. aequatoriale*" Schröder. Jörgensen (1920), who in 1911 had considered Gourret's Fig. 2 as belonging to *C. massiliense* and his Fig. 2a as belonging to *C. carriense* Gourret, proposed the illegal combination "*C. massiliense* (Gourret, Karsten) Jörg.". Sournia (1967), who followed Jörgensen's treatment of Gourret's figures, considered the citation *C. massiliense* (Gour.) Kars. to be invalid, invoking Articles 33 and 34 of the International Code, and cited the combination as "*C. massiliense* (Gour.) Jörg.". But, as it is printed in the "Atlantische Phytoplankton", the combination *C. massiliense* (Gourret) Karsten is validly published. The combination is clearly indicated, with a full reference to the original author, and cannot be considered as an incidental mention. Karsten's species concepts regarding *Ceratium* were often confused, and his wording definitely shows that he considered his two new species and that of Gourret as three separate taxa.

Significant steps in the taxonomic history of this complex up to 1911 are shown in Table 3. Sournia (1966, 1967) recognised the following taxa: *C. massiliense* var. *massiliense*, *C. massiliense* var. *protuberans* (Kars.) Jörg., *C. massiliense* f. *armatum* (Kars.) Jörg., *C. carriense* var. *carriense* Gour. and *C. carriense* var. *volans* (Cl.) Jörg.

No workers have combined *C. massiliense* and *C. carriense*, although many have commented on their great variability and Jörgensen himself (1911) noted that they were confusingly similar. Graham & Bronikowsky (1944) suggested that the two species might be identical, and Wood (1954) observed that there seemed more reason to treat the components of "*C. horridum* (Cl.) Gran" (*C. tenue* O. & S.) as separate species than to divide *C. carriense* from *C. massiliense*. Steemann Nielsen (1939) referred to the *Formenkries* » *massiliense* », which included *C. massiliense*, *C. carriense* and *C. deflexum*. Earlier (1934) he had noted specimens of *C. massiliense* in neritic waters which resembled *C. carriense* var. *carriense* in habit.

An examination of NGY Agulhas current specimens and those depicted in the literature leads to the conclusion that *C. massiliense* and *C. carriense* should indeed be treated as a single species.

The differences between '*C. carriense*' and *C. massiliense* as given by Jörgensen (1911) are as follows: in '*C. carriense*', the antapical horns are far more spreading; the right horn is more divergent, the proximal part making an obtuse angle with the distal part, while in *C. massiliense* this is more of a right angle; the base of the hypotheca is more depressed between the bases of the antapical



FIG. 12.

(Measurements for each specimen given in the following order: girdle diameter, left horn degree co-ordinate with $15\ \mu$ radius co-ordinate, and in I-L, sum of left and right horn MRC's.) A-H, J, K, *C. massillense* var. *massillense* (Gour.) Kars.; A $69\ \mu$, 90° ; B $69\ \mu$, 90° ; C $72\ \mu$, 96° ; D $60\ \mu$, 85° ; E $63\ \mu$, 72° ; F $75\ \mu$, 77° ; G $69\ \mu$, 68° ; H $63\ \mu$, 88° ; J $66\ \mu$, 65° ; K $69\ \mu$, 58° ; 38°; I, *C. deflexum* f. *deflectomassum* Rein.; 60 μ , 70° , 49° ; L, *C. deflexum* f. *deflexum* (Kof.) Jorg.; 63 μ , 55° , 62° ; M, *C. macroceros* (Ehb.) Vanh.; 51 μ , 45° . All specimens from Agulhas current NGY samples, thecal wall shown in optical section and surface view.

horns; the base of the left horn is "less straight", (*gerade*—Jørgensen's meaning is not clear), and makes a definite angle with the base of the hypotheca, which angle is generally smaller than the indistinct angle in *C. massiliense*; the left profile of the hypotheca is straight or weakly convex, while in *C. massiliense* it is somewhat concave and generally oblique; the angle made by projections of the girdle and the base of the hypotheca is smaller, as is the perpendicular distance *B*.

Polar co-ordinate measurements of antapical horn curvature in NGY specimens showed slight discontinuities only in the co-ordinates of the left horn, which delimited three groups; in the first, approximating Jørgensen's concept of *C. massiliense*, the left horn degree co-ordinate with the 150 μ radius co-ordinate was $> 130^\circ$; in the second and third groups, approximating Jørgensen's concept of '*C. carriense*', the left horn was more spreading and the degree co-ordinate with the 150 μ radius co-ordinate was $< 130^\circ$; in the second group, the degree co-ordinate with the 300 μ radius co-ordinate was $> 130^\circ$ and in the third group it was $< 130^\circ$. (See Fig. 11A). While there were no discontinuities in the right horn polar co-ordinates, this horn tended to be more spreading in groups two and three, (see Fig. 11B). Specimens of the first group were found in which the angular delimitation of the base of the hypotheca by the bases of the antapical horns was very marked, (in two such instances, the left horn degree co-ordinates with the 150 μ radius co-ordinates were 143° and 159°), as is the case in a figure of Karsten's (1906 Pl. 22, Fig. 29a) cited by Jørgensen in the synonymy of *C. massiliense*! The left horn degree co-ordinate with the 15 μ radius co-ordinate was $58-97^\circ$, mostly $70-90^\circ$ in group one, and $50-73^\circ$ in groups two and three, while the left horn MBC degree co-ordinate was $63-90^\circ$ in group one, mostly $72-86^\circ$, and $53-73^\circ$ in groups two and three. The left profile of the hypotheca was generally sloping and slightly concave in group one, but this condition was found in some specimens of groups two and three, and straight or slightly convex left profiles, common in groups two and three, were also found in group one. The angle between the base of the hypotheca and the girdle was $22-34^\circ$, mostly $25-31^\circ$ in group one and $19-31^\circ$ in groups two and three. The ratio $\frac{B}{H}$ was $0,14-0,81$, mostly $0,22-0,50$ in group one, and $0,30-0,90$ in groups two and three.

No discontinuities were shown between these groups in measurements of other characters such as girdle diameter, MBC radius co-ordinates, MRC and position of MRC, and the ratios $\frac{L_{90}}{D}$ and $\frac{R_{90}}{D}$.

Measurements of polar co-ordinates of specimens from the literature support these observations, but eliminate the discontinuity between groups two and three, (see Table 4). It is of interest to note that the specimen of unknown size depicted by Pavillard (1905, Pl. 1, Fig. 1) as '*C. volans*' and cited under '*C. carriense*' by Jørgensen (1911), at a diameter of 69 μ , has a value for the left horn degree co-ordinate with the 105 μ radius co-ordinate of approximately 135° , which places it in group one.

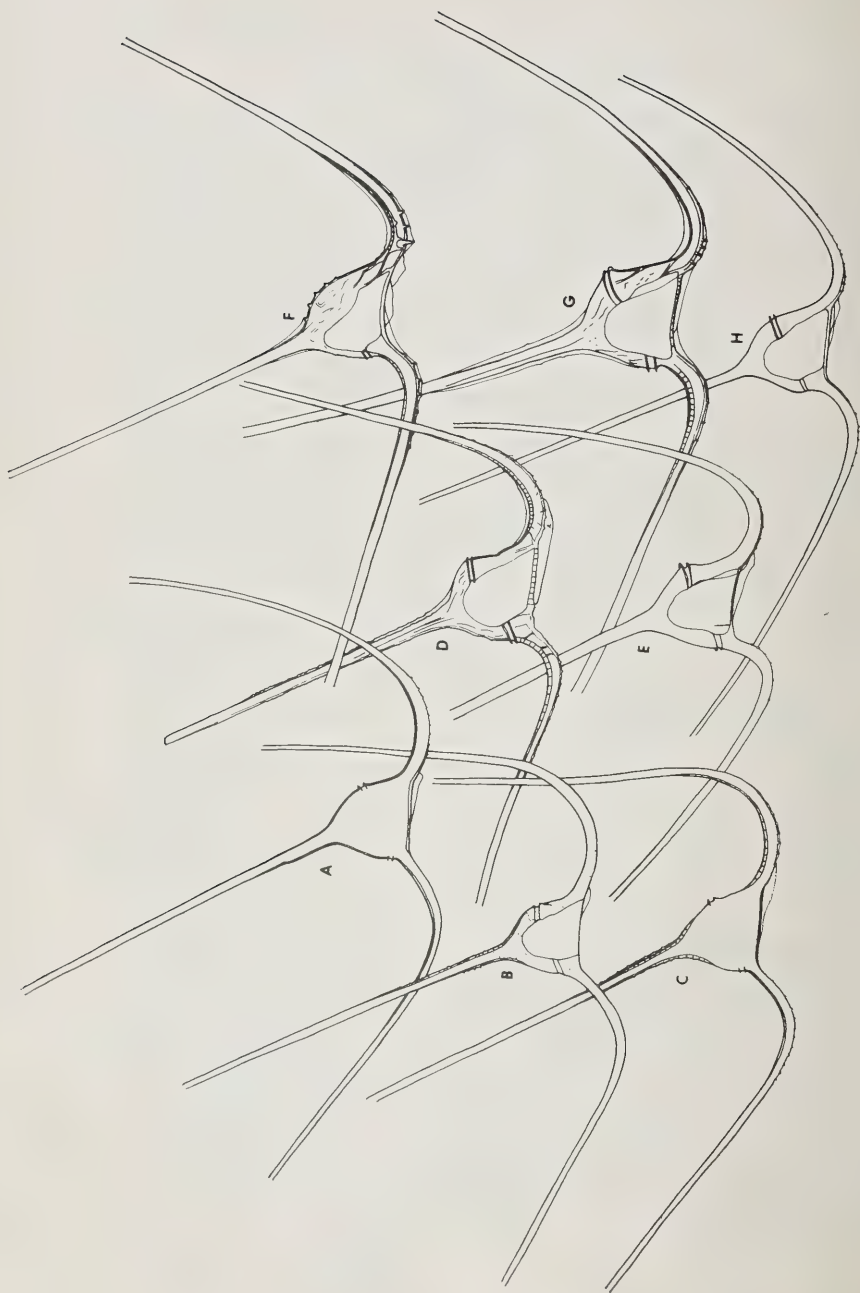


Fig. 13.

(Measurements for each specimen given in this order: girdle diameter, where left horn MRC occurs, and left horn degree co-ordinates with included here to show difference in anapical horn curvature; A: *C. trichoceros* var. *contrarium* (Gour.) Schill.: specimen with diverging anapical horns, 101-120 μ , 65°, 144°, 166°; B: *C. trichoceros* var. *trichoceros* (Gour.) Schill.: specimen with diverging anapical horns, 57-150 μ , 108-120°, 123°, 150°; C: *C. trichoceros* var. *trichoceros* (Gour.) Schill.: specimen with diverging anapical horns, 57-150 μ , 65°, 144°, 166°; D: *C. massiliense* var. *massiliense* (Gour.) Karst.: 69 μ , 45-75°, 77°, 141°, 156°; E: *C. massiliense* var. *massiliense* (Gour.) Karst.: 69-75 μ , 63°, 141°, 156°; F: *C. massiliense* var. *massiliense* (Gour.) Karst.: 72 μ , 30-45°, 60°, 129°, 142°; G: *C. massiliense* var. *massiliense* (Gour.) Karst.: 75 μ , 45-60°, 56°, 119°, 137°; H: *C. massiliense* var. *massiliense* (Gour.) Karst.: 75 μ , 45-60°, 56°, 119°, 137°. All specimens from Agulhas current NGY samples, thecal wall shown in surface view and optical section, horns incompletely shown.

Thus, when the characters, which according to Jörgensen distinguish *C. massiliense* from '*C. carriense*', are actually measured, differences between the two are shown to be far less than warrants their recognition as two separate species, and they are accordingly treated as varieties of a single species.

Ceratium massiliense* var. *massiliense

(See Figs. 12A–H, J, K, 13D, E, 14A, B and 15.)

Sournia (1966): 1982; (1967): 466; Paredes (1969/70): 44, Pl. 22, Fig. 153.

C. massiliense (Gourret) Karsten (1906): 145.

Pavillard (1907): 226; (1916): 17; (1931): 88; Jörgensen (1911): 66, Pl. 7, Figs. 140–142; (1920): 85, Fig. 78; Schröder (1911): 646; Mangin (1912): 24, Fig. 7; Forti (1922): 66, Pl. 3, Fig. 51 (= Jörgensen Fig. 141); Dangeard (1927): 378; Abé (1927): 430, Fig. 48A, B; Paulsen (1930): 89, Fig. 55C–F, *non* A, B (= *C. trichoceros* var. *contrarium* (Gour.) Sch.); Böhm (1931a): 383; Peters (1932): 50, Pl. 1, Fig. 2a, b, Pl. 2, Fig. 10f, Pl. 3, Fig. 13a; Wang & Nie (1932): 301, Fig. 14; Steemann Nielsen (1934): 25, Figs. 60–62; (1939): 14; Nie (1936): 65; Graham & Bronikowsky (1944): 38, Fig. 22E–G, J, K; Silva (1949): 361, Pl. 7, Fig. 3; Margalef & Duran (1953): 42, Fig. 12m–p, ?q, r (figures of an abnormal form of uncertain affinity); Gaarder (1954): 14; Margalef (1957): 48, Fig. 3g; Halim (1960): 180, Pl. 5, Fig. 15; Klement (1964): 357, Pl. 3, Fig. 2; López (1966): 333, Figs. 50, 51; Taylor (1967): 463, Pl. 91, Fig. 39, "intermediate form"; Steidinger & Williams (1970): 46, Fig. 30a–e.

C. tripos var. *massiliense* Gourret (1883): 27, Pl. 1, Fig. 2, *non* 2a (= var. *carriense* (Gour.) Rein.); Daday (1888): 99.

C. tripos var. *macroceras* f. *massiliensis* (Gour.) Schröder (1900): 15.

C. massiliense a *macroceroides* (Kars.) Jörgensen (1920): 86, (used instead of var. or f. *massiliense*).

C. massiliense f. *a macroceroides*: Böhm (1931a): 362; (1931b): 35, Fig. 32a, c, d *non* b (= *C. deflexum* f. *deflectomassum* Rein.).

C. massiliense f. *macroceroides*: Schiller (1937): 424, Fig. 436a; Rampi (1939): 308, Fig. 33; Wood (1954): 308, Fig. 235a; Klement (1964): 357; Halim (1963): 498, Fig. 28.

C. massiliense var. *macroceroides*: Taylor (1967): 463.

C. tripos *macroceroides* Karsten (1906)*: 145, Pl. 22, Fig. 28a, b.

C. massiliense var. *protuberans* (Kars.) Jörgensen (1911): 67, Pl. 7, Fig. 143, Pl. 8, Figs. 144, 145; (1920): 86, Fig. 79; Schröder (1911): 646; Pavillard (1916): 17; Forti (1922): 67, Pl. 4, Fig. 53; Dangeard (1927): 378, Fig. 43b; Graham & Bronikowsky (1944): 38, Fig. 221; Silva (1949): 361; Sournia (1966): 1982; (1967): 467; Paredes (1969/70): 44, Pl. 22, Fig. 154.

C. massiliense f. *protuberans* (Kars.) Böhm (1931a): 362, Fig. 16; (1931b): 35; Schiller (1937): 424, Fig. 463c, d (= Jörgensen Fig. 144); Rampi (1939): 310.

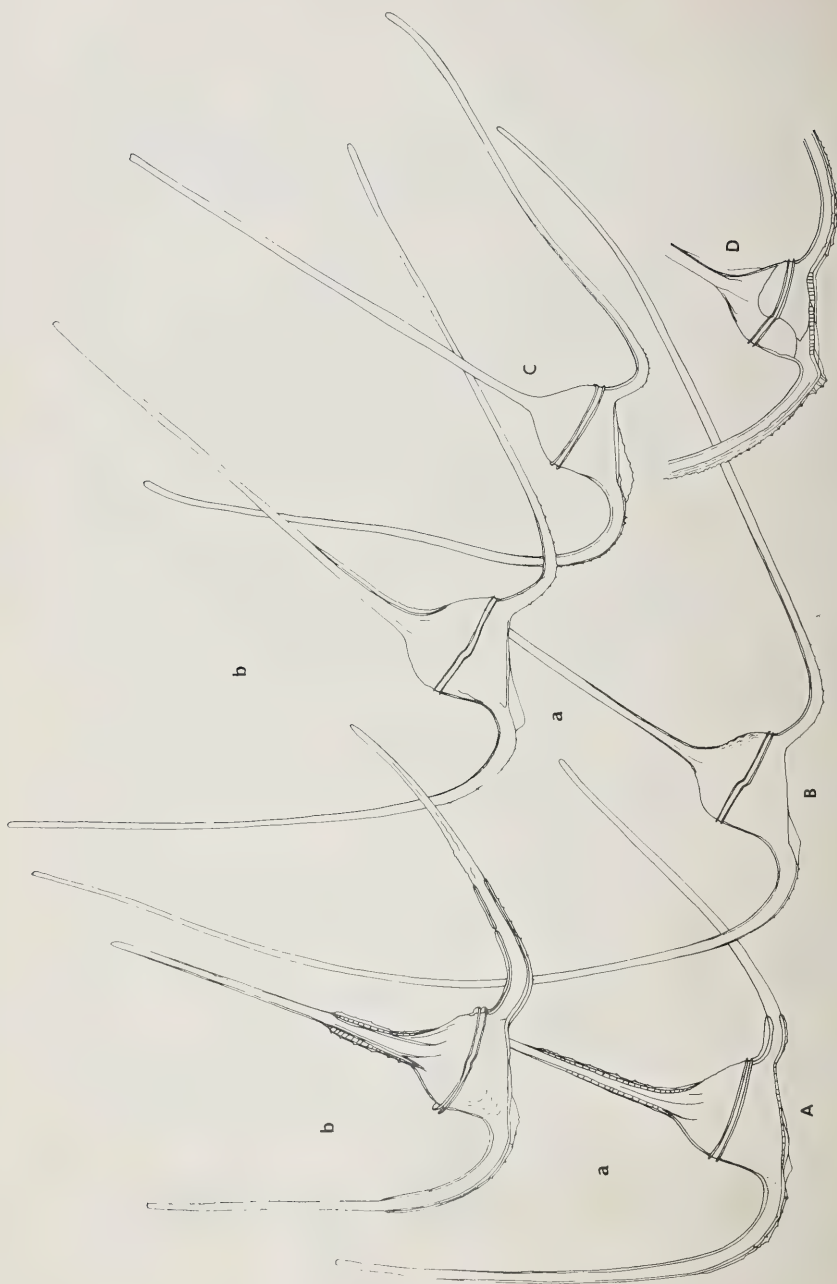


FIG. 14.

(Measurements given for each specimen given in following order: girdle diameter, left horn degree co-ordinate with $15\ \mu$ radius co-ordinate and sum of left and right horn MRC's.) A and B, *C. massiliense* var. *massiliense* (Gour.) Karst.: two celled chains, with regeneration of apical and antapical horns in A, (after autotomy), Aa $66\ \mu$, 89° , 24; Ab $66\ \mu$, 84° , 23; Ba $63\ \mu$, 84° , 23; Bb $66\ \mu$, 70° , 30; C, *C. deflexum* f. *deflexum* (Gour.) Karst.: $66\ \mu$, 70° , 47; D, *C. vultur* f. *sinuatum* (Karst.) Sournia: long apical horned specimen, included to show distinctive base of left horn, $66\ \mu$. All specimens from *Aegulus* current NGY samples, thecal wall shown in optical section and surface view.

Fig. 40; Wood (1954): 308, Fig. 235c; Gaarder (1954): 14; Halim (1960): 180; (1963): 499, Fig. 29.

C. protuberans (Kars.) Paulsen (1930): 89, Fig. 56A-C.

C. tripos protuberans Karsten (1906): 145, Pl. 22, Fig. 27a-g.

C. massiliense f. crassum sensu Jörgensen (1920): 87.

C. tripos macroceras var. *crassa* Karsten (1907): 411, e.p., Pl. 49, Fig. 27a, *non* c, e, (c = *C. macroceras*, e = var. *carriense*).

C. tripos flagelliferum var. *crassa* Karsten (1907): 410, Pl. 49, Fig. 25a-c.

C. massiliense f. armatum sensu Jörgensen (1911): 67, e.p., Pl. 8, Fig. 146; Forti (1922): 67, Pl. 4, Fig. 52 (= Jörgensen Fig. 146); Schiller (1937): 424, Fig. 463b (= Jörgensen Fig. 146); Rampi (1939): 310, Fig. 32; Wood (1954): 308, Fig. 235b; Sournia (1967): 468, Fig. 87 (= Peters (1932) Pl. 3, Fig. 16a), Fig. 88 (= Rampi Fig. 32).

C. massiliense var. *armatum* sensu Peters (1932): 50, Pl. 3, Fig. 16a; Graham & Bronikowsky (1944): 38, Fig. 22L.

Non C. tripos f. macroceras f. armata Karsten (1905): 132, Pl. 19, Figs. 7, 8; (1906): 146, (?) = *C. massiliense f. armatum* (Kars.) Jörg. 1920).

C. massiliense f. ellipticum Böhm (1931a): 362, e.p., Fig. 17a, *non* b, *non* 18a, b (= var. *carriense*).

C. volans sensu Pavillard (1905): 54, e.p., (includes var. *carriense*), Pl. 1, Fig. 1; Okamura (1907)*: 130, e.p., Pl. 4, Fig. 18c, d, e *non* 18a, b (18a = *C. tenue*, 18b = var. *carriense*).

"*C. volans* forma": Schröder (1906)*: 363, Fig. 34.

C. tripos volans var. *campanulata* Karsten (1907): 408.

C. aequatoriale Schröder (1906): 360, Fig. 32; Pavillard (1907): 226.

C. tripos intermedium var. *aequatorialis* (Schr.) Karsten (1907): 412, Pl. 49, Fig. 21a, b.

C. ostenfeldii Kofoed (1907b): 305, e.p., Pl. 26, Figs. 22, 23 *non* 24, 25, (24

C. macroceras, 25 = var. *carriense*).

C. tripos intermedium var. *hundhausenii* sensu Karsten (1907): 413, Pl. 50, Fig. 10, *non C. hundhausenii* Schröder (= var. *carriense*).

C. horridum f. intermedia (Jörg.) Ost.: Okamura (1907): 129, e.p., Pl. 4, Figs. 21a, c *non* b, *non* Fig. 23 (21b = *C. tenue*, 23 = abnormal form of uncertain affinity, probably = *C. macroceras*).

C. horridum f. laevis Okamura (1907)*: 129, e.p., Pl. 4, Fig. 21d, f, h *non* e, g = *C. tenue*, g = *C. contortum* (Gour.) Cl.).

C. horridum subsp. *buceros* var. *molle* sensu Margalef & Duran (1953): 42, Fig. 12j, k.

C. pavillardii sensu Dangeard (1927): 378, Fig. 42a, *non C. pavillardii* Jörgensen (= *C. vulture* var. *pavillardii* (Jörg.) G. & B.).

C. vultur f. regulare Graham & Bronikowsky (1944): 41, Fig. 23C.

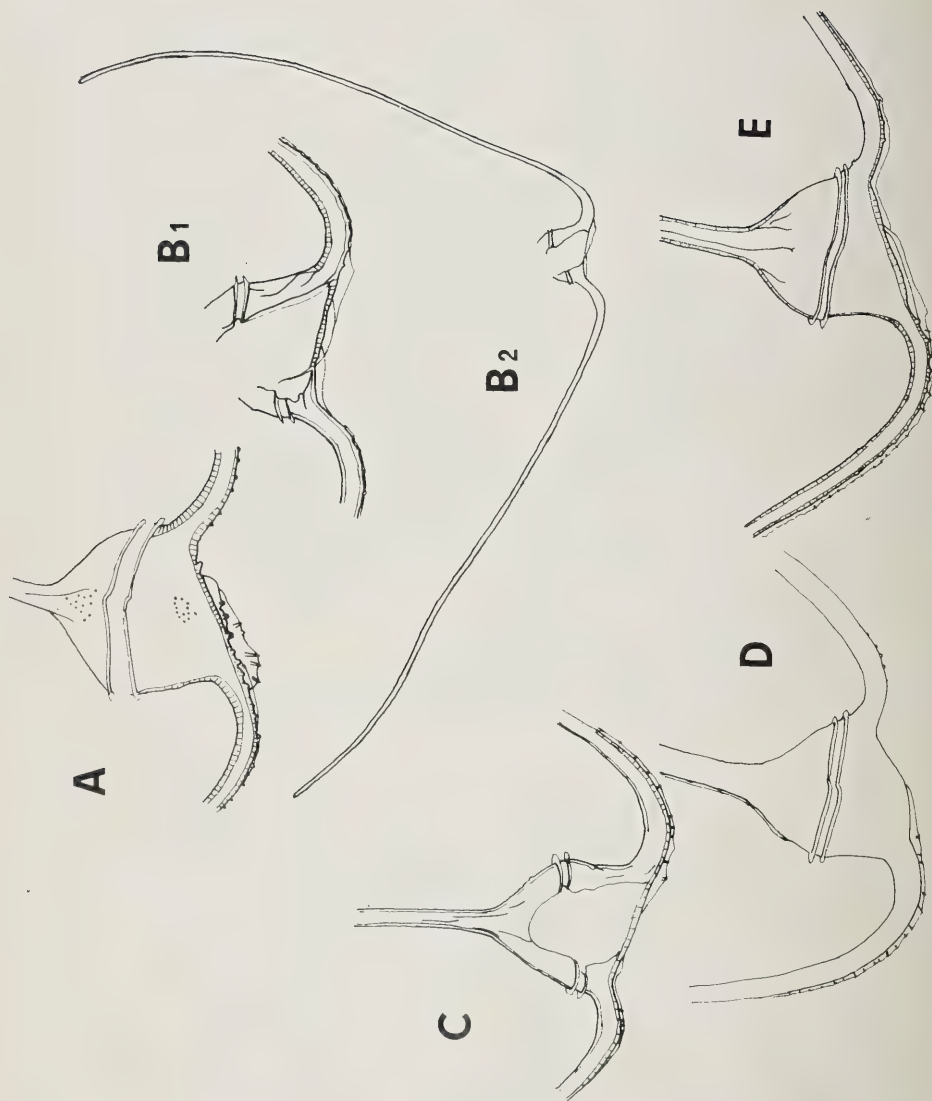


FIG 15
C. massiliense var. *massiliense* (Gour.) Kars.: Showing further variations in antapical spines and lists. Girdle diameter: A 84 μ, specimen broken, B 72 μ, shown at two magnifications, C 69 μ, D 69 μ, E 75 μ. Thecal wall shown in optical section and surface view in all save D, all specimens from Agulhas current NGY samples.

C. contrarium (Gour.) Pav.: Graham & Bronikowsky (1944) e.p., Fig. 22E, non Fig. 24A, B (= *C. trichoceros* var. *contrarium* (Gour.) Sch.).

C. tripos longipes sensu Karsten (1907): 412, Pl. 48, Fig. 11 a, b, Pl. 51, Figs. 12, 13.

C. tripos longipes f. *ventricosa* Karsten (1906): 145, Pl. 21, Figs. 26, 26a.

C. tripos longipes var. *cristata* Karsten (1907): 413, e.p., Pl. 48, Fig. 12c, ? non a, b (? = *f. armatum*).

"*Ceratium* sp." Chun (1903): 64, Fig. b.

C. tripos macroceros sensu Entz (1902) e.p., Pl. 2, Figs. 17, 18, Pl. 6, Figs. 40, 41; sensu Karsten (1906): 145, e.p., Pl. 22, Fig. 29a, non b-d (= *C. macroceros*); (1907): 411, e.p., Pl. 49, Fig. 27a, non b-e (b, c, = *C. macroceros*, d, e = var. *carriense*).

? *C. tripos* var. *macroceros*: Stein (1883) Pl. 16, Fig. 9 (Antapical horns are shown with closed pointed tips, extending to level of about one third of length of apical horn, but left antapical horn definitely curved backwards initially.)

? *C. macroceros*: Wood (1954) e.p., Fig. 238a.

? *C. tripos* var. *macroceras* f. *undulata* Schröder (1900)*: 16, Pl. 1, Fig. 17k, non l, m (l = *C. tenue*, m = *C. vultur* var. *pavillardii*—Jørgensen (1920) cited Fig. 17m in the synonymy of both '*C. pavillardii*' and *C. massiliense*).

? *C. tripos* var. *macroceras* f. *scotica* sensu Schröder (1900): 15, Pl. 1, Fig. 17g; non *C. tripos scoticum* Schütt (1892): 302, Figs. 76 IVc and 91 IV (Fig. 76 IVc = *C. macroceros*, Fig. 91 IV unidentifiable with certainty—Jørgensen (1911) considered it as possibly *C. intermedium* (Jörg.) Jörg. (= *C. tenue*)).

? *C. tripos tergestinum* sensu Karsten (1906): 144, Pl. 21, Fig. 24. (Jørgensen (1911) and Schiller included this in the synonymy of '*var. protuberans*'. The antapical horns are very short, with closed pointed tips, the left horn MBC degree co-ordinate is 90° and the right horn has only a very slight initial backward curvature, so that it might be a badly drawn specimen of *C. tripos* (Müller Nitzsch); non *C. tripos* var. *tergestina* Hensen (= *C. longipes* (Bail.) Gran).

*(Scales given by these authors could be inaccurate, as is certainly the case in Schröder (1900). Okamura has confused *C. tenue* and *C. massiliense* (as has Karsten (1907): 412), and the correct identification of his figures depends upon their girdle diameter. Some of the diameters of figures of Schröder (1906) and Karsten are far larger than any encountered in NGY Agulhas current specimens.)

Diagnosis: Differs from var. *carriense* in that the left horn degree co-ordinate with the 150 μ radius co-ordinate is $> 130^\circ$. (Differs from *f. armatum* in that spines are not always present along the lower margins of the antapical horns, and if they are present, these spines decrease in size distally, so that at the level of the base of the apical horn they are absent or minute.)

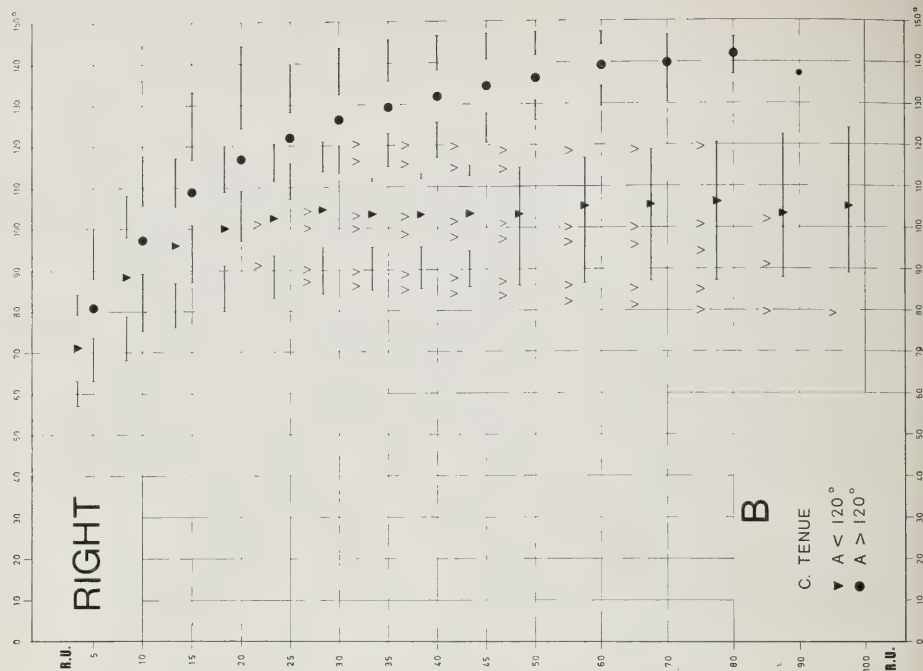
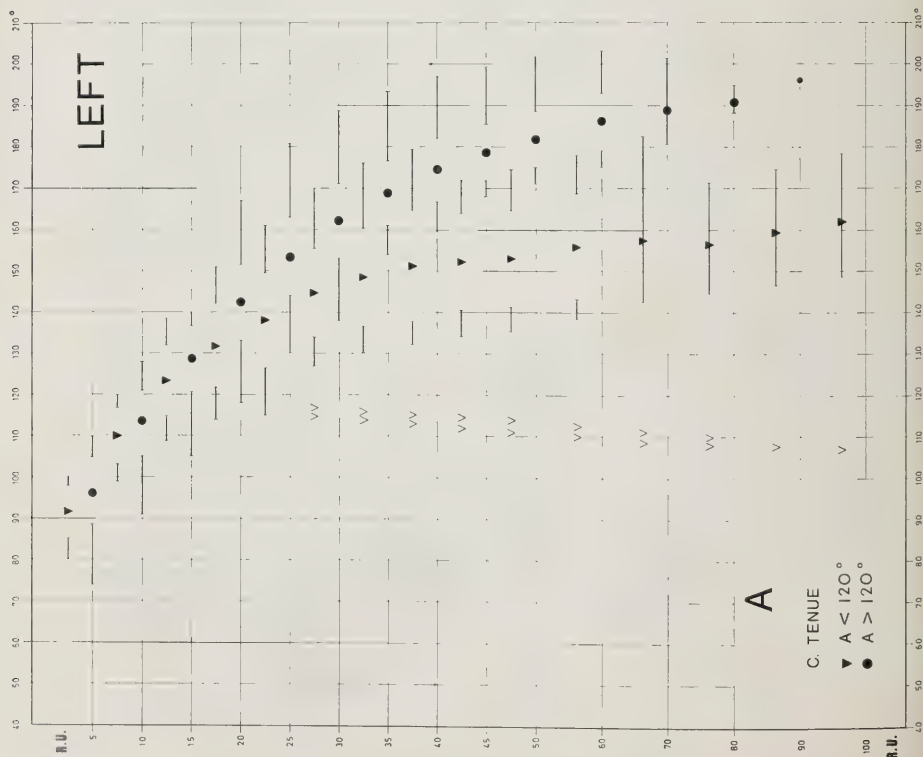
Taxonomic history and present treatment: Karsten (1906) described his two new

species *C. tripos protuberans* and *C. tripos macroceroides* (treated by Jörgensen as *var. massiliense*) thus: "Man sieht die Scheitellinie fast oder doch nur mit geringem Absatz auf das linke Antapikalhörn übergehen, während das rechte deutlich über diese Grenze nach unten verstößt . . . Sie mögen als *Ceratium tripos protuberans* n. sp. benannt . . . Fig. 27a–g, Taf. XXII . . . *Ceratium tripos macroceroides* n. sp. Fig. 28, Taf. XXII . . . welches bereits beide Antapiklhörner über die Scheitellinie hinausstrekt, aber noch nicht die Knickung im Ansatz des linken Antapikalhornes zeigt, die für *macroceras* selbst charakterisch ist."

Jörgensen (1911) distinguished between *C. massiliense* and '*C. massiliense var. protuberans*' thus: in '*var. protuberans*', which is generally slightly larger, the left horn is laterally directed from its inception and its base is not, or indistinctly, delimited from the base of the hypotheca; the angle made by the bases of the left horn and the hypotheca is larger, mostly 180° ; the distance *B* is small; the proximal parts of the antapical horns are very stout, the distal parts frequently long and thin; the base of the hypotheca is mostly distinctly convex in ventral view; the profile of the epitheca is more convex; the left profile of the hypotheca is almost straight; the theca is usually thickened and the apical horn is mostly somewhat curved.

Using these criteria, however, it is impossible to distinguish two distinct taxa, as Jörgensen did, in the specimens depicted in Karsten's Figs. 27 and 28. In Fig. 27a and c–g, the left horn MBC degree and radius co-ordinates are 90° and zero, while in Figs. 27b and 28, these co-ordinates are $< 90^\circ$ and > 0 ; in all, the bases of the antapical horns are of a similar thickness; in Fig. 27d, the base of the hypotheca in ventral view is straight; there is little difference in body shape between Figs. 27 and 28, and the apical horn is not curved at the base in all specimens of Fig. 27; the specimens of Fig. 27a and b and Fig. 28 are similar in size, but those in Fig. 27c–g are larger. (Jörgensen did query the inclusion of Fig. 27a and b in '*var. protuberans*', but did not indicate to which other taxon they might belong.)

Peters (1932) considered that only *var. armatum* should be recognised as an infraspecific taxon of "*C. massiliense massiliense*", as it occurred in cooler waters than the other previously described components of this species, in which he included "*C. inflexum* (Gour.) Jörg." (= *C. trichoceros*), *C. deflexum* and '*var. protuberans*', all of which he found had the same distribution in the S. Atlantic. Steemann Nielsen (1934) appears to have regarded the subdivision of *C. massiliense* as unnecessary, for he found many intergrades. He found only "*a-macroceroides-like*" forms in the warmest parts of the S. Equatorial current and only *protuberans*- and *armatum*-like forms in temperate waters off New Zealand, but mixed "*macroceroides-protuberans*" populations in other warm parts of the S. Pacific. Graham & Bronikowsky (1944) reported nine recognisable varieties of *C. massiliense* in the Carnegie samples, with intergrades, de-



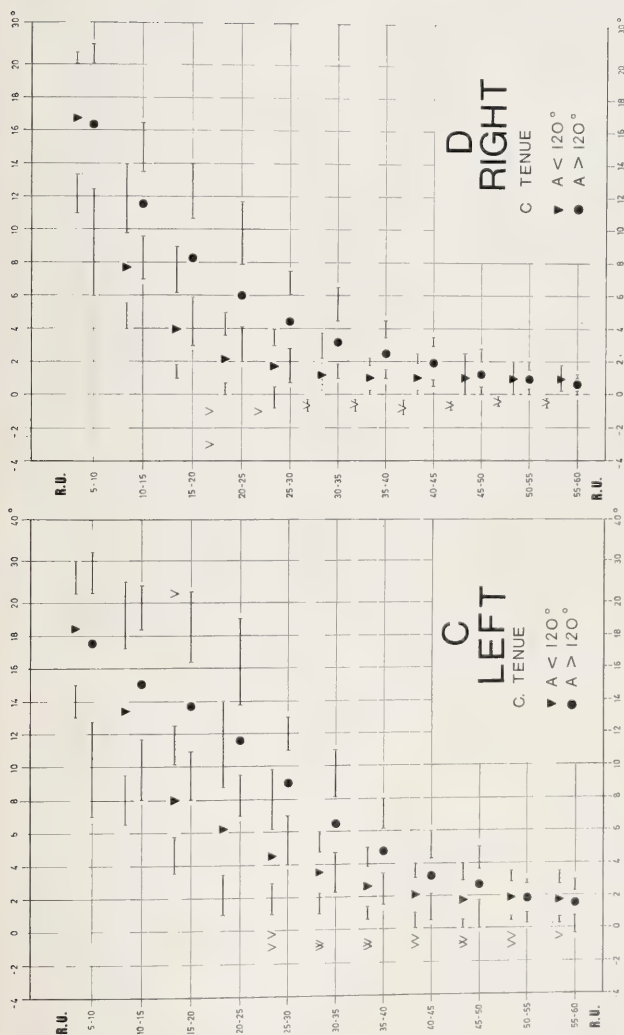


FIG. 17A-D.

C. tenuis Ost. & Schm.: Antapical horn curvature in specimens from Agulhas current NGY stations. A, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; B, the same for the right horn; C, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5-10 to 55-60 R.U.; D, the same for the right horn. A = right horn degree co-ordinate with 150 μ (50 R.U.) radius co-ordinate. See Key to Fig. 5; here the V's represent specimens with re-curved horns.

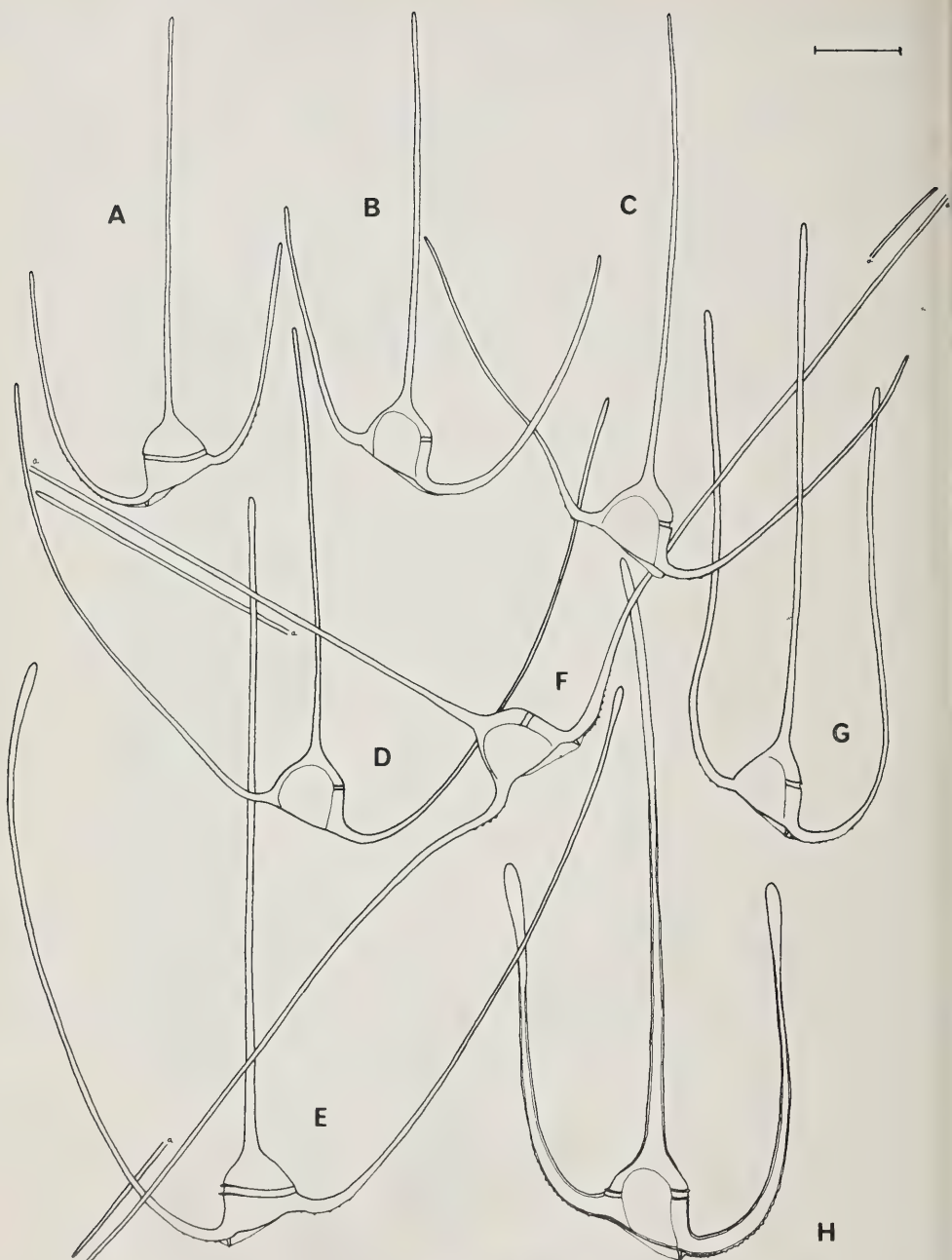


FIG 18.
C. tenue Ost. & Schm.: specimens from Agulhas current NGY stations; the scale line
indicates 42 μ .

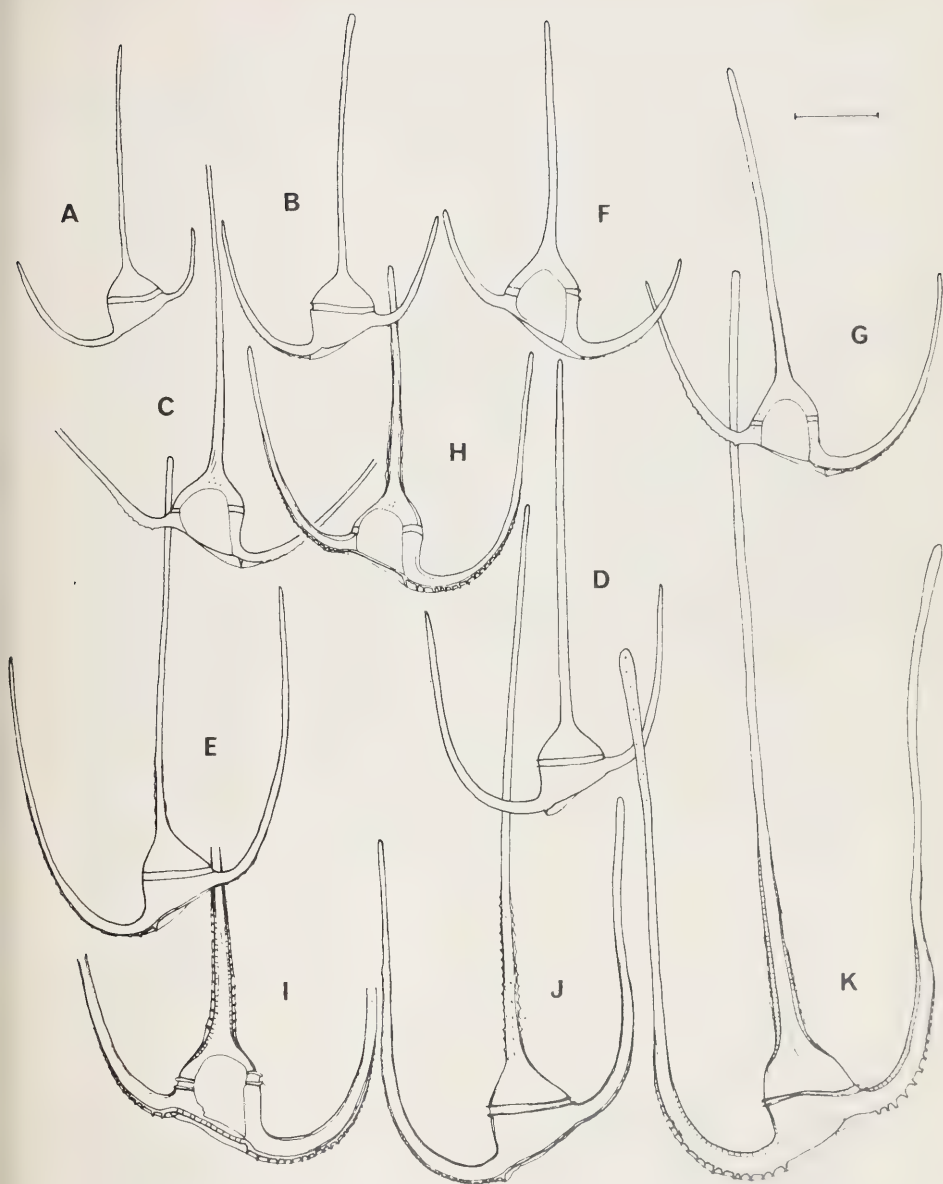


FIG. 19.

C. tenue Ost. & Schm.: specimens from Agulhas current NGY stations; the scale line indicates 42 μ .

scribed the habit of only eight, and named only *var. massiliense*, '*var. protuberans*' and *var. armatum*. They found no correlation between these varieties and hydrographic conditions. Sournia (1967) found that it was always possible to distinguish between *var. massiliense* and '*var. protuberans*' in his samples, from which *f. armatum* was absent.

In the Aghulas current NGY samples, specimens resembling Jørgensen's figures of both *var. massiliense* and '*var. protuberans*' were found. There was no discontinuity in the polar co-ordinate measurements of antapical horn curvature in these, in particular the left horn degree co-ordinates at MBC and with the 15 μ radius co-ordinate. Body shape, size, thickness of antapical horn bases and curvature of the apical horn varied independantly of these co-ordinates.

The maintenance of *var. protuberans* as a separate infraspecific taxon is indeed unwarranted.

Description: Antapical horn curvature: In specimens examined, antapical horns sometimes very slightly deflected ventrally, distal parts of horns sometimes slightly undulating, sometimes curving outwards. Polar co-ordinate measurements of horn curvature: *Left horn:* Varies from being latero-anteriorly directed at inception, when MBC degree and radius co-ordinates are 90° and zero, to having an initial backward curvature, with MBC co-ordinates varying to 63° and 42 μ , mostly 73–86° and 8–26 μ , when its base makes an indistinct to an obvious angle with that of the hypotheca; degree co-ordinate with 15 μ radius co-ordinate 55–100° (> 100° in Karsten's *C. tripos intermedium var. hundhausenii*); with 105 μ , 120–149°, mostly 130–144°; with 150 μ , 134–174°, mostly 140–164°; with 300 μ , 145–184°; MRC occurs between 15 and 75 μ radius co-ordinates, (in only one case between 75 and 90 μ) and is 9–25°, mostly 10–17°; $\frac{L_{90}}{D}$ 0,00–0,91, mostly 0,25–0,63; $\frac{B}{H}$ 0,00–0,81, mostly 0,22–0,50.

Right horn: Always curved backwards initially, making a rounded to a pointed angle with base of hypotheca; MBC degree co-ordinate 45–72°, mostly 50–65°, always less than in left horn, MBC radius co-ordinate 25–60 μ , mostly 33–50 μ , always greater than in left horn; degree co-ordinate with 15 μ radius co-ordinate 20–70°, mostly 30–55°, always less than in left horn; with 150 μ , 85–125°; with 300 μ , 95–125°; MRC occurs between 15 and 75 μ radius co-ordinates and is 10–22°, mostly 10–18°; $\frac{R_{90}}{D}$ 0,69–2,20, mostly 0,90–1,75. Sum of left and right horn MRC's 20–39°, mostly 22–33°. (See Fig. 11.)

Dimensions: In NGY specimens: Girdle diameter 60–84 μ , mostly 63–73 μ ; length hypotheca 36–54 μ ; length epitheca 24–42 μ ; length apical horn 132–645 μ (90 μ in one specimen, which could have been broken); angle made by projections of hypotheca base and girdle 22–34°. *From literature:* diameter 62–85 μ (Jørgensen 1911); 92 μ (Wang & Nie 1932); up to 81 μ (Steemann Nielsen 1934 —he gives the range of measurements as 55–81 μ , but specimens < 60 μ are

here regarded as belonging to *C. tenue*; Nielsen found no correlation between diameter and temperature); 79 μ (Nie 1936); 61–122 μ (Steidinger & Williams 1970); length apical horn: up to 650 μ , angle between hypotheca base and girdle 27–33° (Jørgensen 1911). *Length antapical horns*: horn length variable and difficult to determine as horns often broken (or autotomised?); specimens seen in which antapical horns extend beyond level of top of apical horn and in others, antapical horns have closed rounded tips and extend to level of mid apical horn length. (See Fig. 10.)

Thecal ornamentation: Thecal walls smooth or thickened and ridged. Apart from sulcal list along left side of sulcus, up to three lists found along base of hypotheca: one, sometimes only list present, in angle between hypotheca and left horn, extending along hypotheca base for about two thirds of length of base and a little way onto base of left horn, sometimes continuing along lower margin of left horn, usually supported by small spines and gradually decreasing in width, to level of girdle; a second along base of sulcus; third in angle between base of right horn and hypotheca, extending up to halfway along hypotheca base and a very little way onto base of right horn, occasionally continuing long right horn as for left horn; sometimes additional lists found along lower edges of antapical horns, more rarely along right horn, situated along horns as already described. Margins of lists smooth to serrated; sometimes serrations of lists along hypotheca base thickened into denticles. Spines, if present along lower edge of antapical horns, sometimes stouter and longer in region of recurvature, diminishing in size to insignificance at level of base of apical horn. Occasionally, smooth margined lists, extending for a very short distance, found along upper margins of bases of antapical horns. Apical horn smooth, or ornamented at base with minute spines along plate sutures; sometimes a list present on one or both sides at base, seen in full dorsal or ventral view, with smooth to serrated margins, occasionally supported by spines. Tips of antapical horns sometimes slightly inflated.

TAXON INCERTAE SEDIS

C. massiliense* f. *armatum (Karsten) Jørgensen (1920): 87.

Ex parte: Schiller (1937): 424, *non* Fig. 436b (— Jørgensen (1911) Fig. 146); Rampi (1939): 310, *non* Fig. 32; Wood (1954): 308, *non* Fig. 235b; Sournia (1967): 468, *non* Figs. 87, 88 (= Rampi Fig. 32, Peters (1932) Fig. 16a). (all *var. massiliense*).

C. massiliense *var. armatum* (Karsten) Jørgensen (1911) e.p.: 67, *non* Pl. 8, Fig. 146; Peters (1932): 50, *non* Pl. 3, Fig. 16a; Graham & Bronikowsky (1944): 38, *non* Fig. 22L, (all = *var. massiliense*); Sournia (1966): 1982.

C. tripos *var. macroceras* f. *armata* Karsten (1905): 132, Pl. 19, Figs. 7, 8

C. tripos longipes var. *cristata* Karsten (1907): 413, e.p., Pl. 48, Fig. 12a, b non c (= var. *massiliense*).

Diagnosis: Distinguished by the presence of long spines along the lower edges of the antapical horns; these spines are still very prominent at the level of the base of the apical horn. Differs from specimens of *C. tenue* with very spiny antapical horns only on grounds of size, the girdle diameter here being $> 60 \mu$.

The relationship between *C. massiliense* var. *massiliense* and the specimens described by Karsten as *C. tripos* var. *macroceras* f. *armata*, and *C. longipes* var. *cristata*, included in the synonymy of var. *armatum* by Jörgensen (1911) is problematic. Karsten's iconotype of f. *armata* shows a var. *massiliense*-like individual in which the left horn MBC degree co-ordinate is 90° , the antapical horns are not much longer than twice the body length and have tapered rounded tips. Both apical and antapical horns are ornamented for about three quarters of their length, beyond the level of the base of the apical horn, by lists which are supported by longish stout spines, which do not decrease much in size distally, are relatively long at the level of the base of the apical horn and are more like the spiny lists found in some specimens of *C. tenue*. Karsten later (1906: 146) considered f. *armata* to belong to "*C. tripos horridum*" (= *C. tenue*). However, the girdle diameter of Figs. 7 and 8, calculated from the somewhat confusing scale, appears to be larger than 65μ , which is too big for *C. tenue*. The specimens of var. *cristata* of Fig. 12a, b, with a left horn MBC degree co-ordinate $< 90^\circ$, have smooth lists along the proximal part of the apical horn and spiny lists along the base of the hypotheca as well as the lower margins of the antapical horns. The spines are also largish and more typical of *C. tenue*; they decrease in size distally, but are still quite long beyond the level of the base of the apical horn. The antapical horns are truncated. The specimen in Fig. 12c, described as having a newly formed antapical half, lacks any lists or spines on the antapical horns and hypotheca base.

Other specimens depicted by Karsten and attributed to var. *armatum* by Jörgensen are: "*C. tripos longipes* f. *ventricosa*" (1906) and "*C. tripos longipes*" (1907, Pl. 51, Figs. 12, 13). Later original figures of specimens referred to as var. or f. *armatum* are those of Jörgensen (1911), Peters (1932 Pl. 3, Fig. 16b) who depicts another specimen with virtually identical lists and spines as "*C. massiliense* . . . robust" in Pl. 1, Fig. 2b, Rampi (1939), Graham & Bronikowsky (1944) and Wood (1954). In none are the antapical horn lists supported by spines as described above. The apical horns are shown without lists, or with lists on either side of the base or proximal part, which are smooth, serrated or supported by spines. The proximal parts of the antapical horns have denticle-like spines or lists supported by spines, which are smaller than those depicted by Karsten in f. *armata* and 'var. *cristata*'; they are longest in the region of recurvature and

decrease in size distally, so that at the level of the base of the apical horn they are minute or absent. In one instance denticle-like spines are shown along the base of the hypotheca. In Karsten's figure of *f. ventricosa*, the antapical horns are similar to those depicted in his *f. armata*, while in the other figures mentioned, they are long or obviously truncated. *C. massiliense f. armatum* is mentioned, without any figures, by Jörgensen (1920), Gaarder (1954), Taylor (1967), and as *C. macroceras f. armata* by Nel (1968).

NGY specimens were found with horn ornamentation as just described, save that in no instances were the lists of the apical horns traversed by supporting spines. There was a complete gradation in antapical horn ornamentation to smooth antapical horns lacking lists along the lower margins.

Apart from Karsten's figures of *f. armata* and '*var. cristata*' (Fig. 12a, b) the specimens depicted in the literature and named or cited as "*C. massiliense f. or var. armatum* (Kars.) Jörg." are here regarded as specimens of *var. massiliense*. The true position of Karsten's *f. armata* and '*var. cristata*' is uncertain.

C. massiliense var. carriense (Gourret) Reinecke comb. nov. (See Figs. 13 F-H and 16.)

C. carriense Gourret (1883): 38, Pl. 4, Fig. 57; Jörgensen (1911): 68, Pl. 8, Fig. 147a, b; (1920): 89, Fig. 81; Schröder (1911): 646; Forti (1922): 68, Pl. 4, Fig. 54; Paulsen (1930): 90; Peters (1932): 50, Pl. 2, Fig. 10h; Schiller (1937): 425, Fig. 464a (= Jörgensen 147a), b; Rampi (1939): 310, Fig. 35; Graham & Bronikowsky (1944): 39, Fig. 22A; Wood (1954): 308; Halim (1960): 179; López (1966): 333, Figs. 47, 48; Steidinger & Williams (1970): 44, Fig. 13a, b.

C. carriense: Steemann Nielsen (1934): 26; (1939): 14.

C. carriense var. carriense: Sournia (1966): 1982; (1967): 470.

C. carriense f. eucarriense Böhm (1931a): 363.

C. carriense var. volans (Cleve) Jörgensen (1911): 70, Pl. 8, Figs. 148a, b, 149a, b; (1920): 90; Schröder (1911): 646; Pavillard (1916): 17, Pl. 1, Fig. 4; (1931): 89; Forti (1922): 69, Pl. 4, Fig. 55 (—Jörgensen Fig. 149a); Dangeard (1927): 378; Paulsen (1930): 90, Fig. 57A–D; Steemann Nielsen (1934): 26, Fig. 64; Silva (1955): 172, e.p., Pl. 9, Figs. 6–8, *non* 5 (= *C. tenue* on account of size); Sournia (1966): 3; (1967): 470; Steidinger & Williams (1970): 44, Fig. 14a, b. *C. carriense f. volans* (Cleve) Böhm (1931a): 363; Peters (1932): 50; Schiller (1937): 426, Fig. 465 (= Jörgensen Fig. 149a); Rampi (1939): 310, Fig. 37; Wood (1954): 309, Fig. 236a; Halim (1960): 79, Pl. 5, Fig. 11; (1963): 499.

C. carriense subsp. volans (Cleve) Margalef & Duran (1953): 42, Fig. 121.

C. carriense volans: López (1966): 333, Fig. 49.

C. carriense "carriense-volans": Sournia (1966): 1982, (1967): 471.

*(See comment under *var. massiliense*.)

- C. (tripos* var. ?) *volans* Cleve (1900a): 15, Pl. 7, Fig. 4.
C. tripos volans: Karsten (1906)*: 144, Pl. 21, Fig. 19a, b, 20, 20a.
C. volans (Cleve) Ostenfeld & Schmidt (1901): 168, Fig. 21; Pavillard (1905): 54, e.p., non Pl. 1, Fig. 1 (= var. *massiliense*); Pavillard (1931) Pl. 3, Fig. 5A; Okamura (1907)*: 130, e.p., Pl. 4, Fig. 18b, non a, c-e (18a = *C. tenue*, c-e = var. *massiliense*).
Non "C. *volans* forma": Schröder (1906)*: 363, Fig. 34 (= var. *massiliense*).
C. volans var. *elegans* (Schröder) Pavillard (1931) Pl. 3, Fig. 5B.
C. tripos volans var. *elegans* (Schröder) Karsten (1907): 409, Pl. 49, Fig. 18a, b.
C. elegans Schröder (1906): 364, Fig. 36.
C. carriense var. *volans* f. *rectangulatum* Jörgensen (1920): 90, Fig. 82, (= Jörgensen Fig. 148a).
C. carriense var. *volans* f. *parallela* Pavillard (1923): 916, Fig. C.
C. tripos volans f. *strictissima* Karsten (1906): 144, Pl. 21, Fig. 21.
C. tripos volans var. *tenuissima* Karsten (1907): 409, e.p., Pl. 49, Fig. 17b, non a (= *C. tenue*).
Non *C. tripos volans* f. *recurvata* Karsten (1906): 144, Pl. 21, Fig. 22 (= *C. tenue*).
C. carriense f. *ceylanicum* (Schröder) Jörgensen (1911): 70, Pl. 8, Fig. 150a, b; Böhm (1931a): 363; (1931b): 37; Peters (1932): 50; Steemann Nielsen (1934): 27; Schiller (1937): 427; Wood (1954): 309, Fig. 236b; Gaarder (1954): 11.
C. carriense var. *ceylanicum* (Schröder) Schröder (1911): 647.
C. ceylanicum Schröder (1906): 363, Fig. 35; Pavillard (1931): 92, Pl. 3, Fig. 6.
C. carriense f. *hundhausenii* (Schröder) Wood (1954): 309.
C. hundhausenii Schröder (1906): 364, Fig. 37; non Pavillard (1931) Pl. 3, Fig. 7 (= *C. macroceros*).
Non *C. tripos intermedium* var. *hundhausenii* Karsten (1907): 413, Pl. 50, Fig. 10 (= var. *massiliense*).
C. tripos var. *massiliense* Gourret (1883): 27, e.p., Pl. 1, Fig. 2a non 2 (= var. *massiliense*).
C. massiliense f. *ellipticum* Böhm (1931a): 362, e.p., Fig. 17b, non a, 18a, b, (Fig. 17b = var. *massiliense*).
C. patentissima Ostenfeld & Schmidt (1901): 168, Fig. 22.
C. patentissimum: Pavillard (1907): 226, Fig. 1A, B; Okamura (1907)*: 130, Pl. 3, Fig. 2a-c.
Non *C. tripos patentissimum*: Karsten (1906): 144, Pl. 21, Fig. 23, 23a (= *C. tenue*).
C. ostenfeldii Kofoid (1907b): 305, e.p., Pl. 26, Fig. 25, non 22-24 (22, 23 = var. *massiliense*, 24 = *C. macroceros*).
C. tripos macroceros: Entz (1902) e.p., Pl. 6, Fig. 42; Karsten (1907): 411, e.p., Pl. 49, Fig. 27d, non b (= *C. macroceros*).

*(See comment under var. *massiliense*)

C. tripos macroceras var. *crassa* Karsten (1907): 411, e.p., Pl. 49, Fig. 27e, non a, c (a = var. *massiliense*, c = *C. macroceros*).

"*Ceratium* sp." Chun (1903): 64, Fig. a.

Diagnosis: Differs from var. *massiliense* (and *f. armatum*) in that the left horn degree co-ordinate with the 150 μ radius co-ordinate is $< 130^\circ$.

Taxonomic history and present treatment: Jörgensen (1911) separated *C. carriense* from '*C. carriense* var. *volans*' on the grounds that in *C. carriense* the antapical horns are stouter, less spreading, usually more coarsely denticulate, with the right horn more evenly curved; the base of the hypotheca is more depressed between the antapical horns; the angle made by projections of the girdle and hypotheca base is larger; the left profile of the hypotheca is more oblique and the right profile of the epitheca is more convex.

In neither Gourret's figure of *C. carriense* nor Cleve's figure of *C. volans* can the spread of the antapical horns be determined, because only the proximal parts are shown. In both figures, the antapical horns are of similar thickness and the left profile of the hypotheca is oblique; in Cleve's figure, the antapical horns are ornamented with coarsely serrated lists, in Gourret's, lists and spines are absent; the right horn MRC occurs approximately between the 30 and 45 μ radius co-ordinates in Cleve's figure, and approximately between the 30 and 60 μ co-ordinates in that of Gourret.

As Gourret's specimen of *C. carriense* is drawn tilted, the true degree of depression of the hypotheca base between the antapical horns cannot be determined and polar co-ordinate measurements are not accurate. A comparison of Jörgensen's Fig. 147b of '*C. carriense*' and 148b of '*C. carriense* var. *volans*' shows an identical degree of depression of the hypotheca base, almost the same angle between the girdle and hypotheca base, and the right profile is more convex in Fig. 148b. In Paulsen's Figs. 57A and C of '*C. carriense* var. *volans*' the right horn is as evenly curved as in Gourret's Fig. 57.

Graham & Bronikowsky (1944) did not subdivide *C. carriense* into varieties because of the numerous intergrades. Steemann Nielsen (1939) wrote: "Es ist die ursprüngliche Varietät *volans* (Cleve), die ich unter dem Namen *C. carriense* angebe. Die ursprüngliche Hauptart ist wohl meistens zum Artenkomplex *C. massiliense* mitgerechnet worden." Sournia (1966, 1967), while retaining var. *carriense* and 'var. *volans*', recognised the presence of intermediates, which he named, unconventionally, "*carriense-volans*". From the values of their left horn degree co-ordinates with the 150 and 300 μ radius co-ordinates, the specimens depicted in the literature which are cited by Sournia as intermediates, represent all three of the previously mentioned groups found in the NGV specimens.

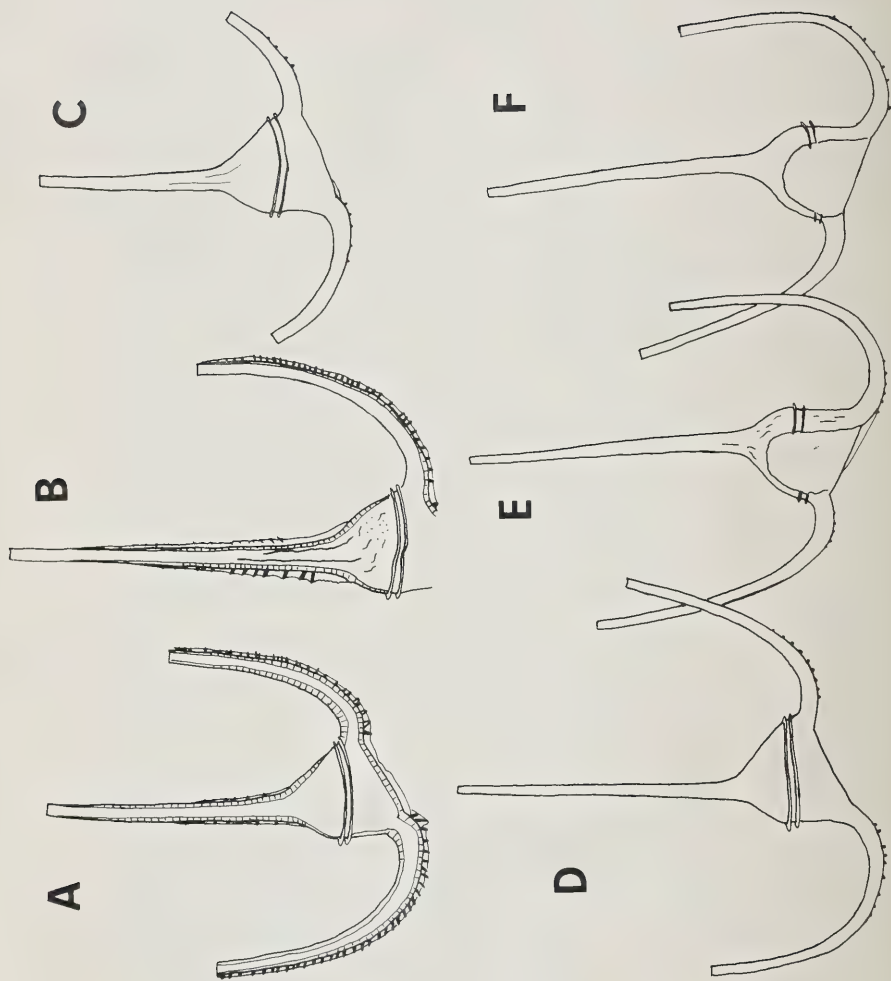


Fig 20 station NGY 41, (see page 70); D-F, specimens from Oslo Fjord. Girdle diameters: A 48 μ , B 54 μ , C 48 μ , D 54 μ , E 48 μ , F 48 μ .

C. tenue Ost. & Schm.: A-C, specimens from Agulhas current; D-F, specimens from

It has been noted that the polar co-ordinate measurements of antapical horn curvature of specimens from the literature blurred the discontinuity between the two groups of NGY specimens approximating Jörgensen's concept of *C. carriense*. The subdivision of *var. carriense* into two taxa is indeed unjustified. It is of interest to note that, had two varieties been recognised, based on the left horn degree co-ordinate with the 300 μ radius co-ordinate, in specimens in which the left horn degree co-ordinate with the 150 μ radius co-ordinate was $< 130^\circ$, the epithets '*carriense*' and '*volans*' would have had to have been discarded.

Description: Antapical horn curvature: In specimens examined, both horns always curved backwards initially, left horn base making an indistinct to an obvious angle with the base of the hypotheca, usually the latter; horns long and disposition of distal parts very variable, often differing in right and left horns of same specimen; distal parts may be spreading to roughly parallel to the apical horn, sometimes recurved posteriorly, sometimes slightly undulating. *Polar co-ordinate measurements of curvature: Left horn:* MBC co-ordinates $60-84^\circ$, usually $60-80^\circ$, and $9-57 \mu$, mostly $15-45 \mu$; degree co-ordinates with 15 μ radius co-ordinate $50-85^\circ$, very rarely $< 50^\circ$, mostly $50-70^\circ$; with 105 μ , $79-123^\circ$, mostly $95-115^\circ$; with 150 μ , $93-129^\circ$, mostly $100-125^\circ$; with 300 μ , $108-151^\circ$; MRC occurs between 15 and 75 μ radius co-ordinates, very rarely beyond 75 μ , and is $6-27^\circ$, mostly $7-15^\circ$; $\frac{L_{90}}{D}$ 0.21-1.73, mostly 0.40-1.25; $\frac{B}{H}$ 0.20-1.42, mostly 0.30-0.90. *Right horn:* MBC degree co-ordinate $47-84^\circ$, mostly $50-80^\circ$, up to about 20° greater or less than in left horn; MBC radius co-ordinate very variable, $18-492 \mu$, mostly $37-150 \mu$, slightly less, to up to 480 μ greater, than in left horn; degree co-ordinate with 15 μ radius co-ordinate $20-80^\circ$, mostly $35-65^\circ$, up to 25° less, and 43° greater, than in left horn; degree co-ordinate with 105 μ radius co-ordinate $60-110^\circ$, mostly $65-95^\circ$; with 150 μ , $70-110^\circ$; with 300 μ , $75-125^\circ$; MRC occurs between 15 and 75 μ radius co-ordinates, very rarely beyond 75 μ , and is $3-14^\circ$, (20° recorded in one case), mostly $3-10^\circ$; $\frac{R_{90}}{D}$ very variable, 1.30-10.48 (0.81 recorded in a single case). Sum of left and right horn MRC's $12-33^\circ$, (about 47° in Jörgensen's figure of '*C. carriense f. ceylanicum* (Schr.) Jörg.', (1911) Fig. 150). (See Fig. 11.)

Dimensions: In NGY specimens: girdle diameter $60-78 \mu$; length hypotheca $39-54 \mu$; length epitheca $21-42 \mu$; length apical horn $285-750 \mu$; angle made by projections of hypotheca base and girdle $19-31^\circ$. *From literature:* diameter $63-77 \mu$ (Jörgensen 1911), up to 148μ (Steidinger & Williams 1970—they give range of measurements as $56-148 \mu$, specimens $< 60 \mu$ in diameter are here treated as belonging to *C. tenue*); length apical horn $300-875 \mu$, angle between hypotheca base and girdle $20-27^\circ$ (Jörgensen 1911). (See Fig. 10.)

Thecal ornamentation: As in *var. massiliense*; thecal wall generally not heavily thickened and extreme development of lists and spines not usually found;

specimens with initially very spreading antapical horns tend to have smooth horns and apart from the sulcal list, only a list between the base of the left horn and hypotheca.

Distribution: The distribution of *C. massiliense* in NGY Agulhas current stations is shown in Tables 1 and 2. In specimens from this area, there appeared to be no correlation between variation in size, antapical horn curvature and thecal ornamentation and temperature and neritic and oceanic conditions. Previous records for this area are those of Taylor (1967), as '*C. carriense f. carriense*' and '*f. volans*' and '*C. massiliense var. armatum*', "*C. massiliense* intermediate form" and '*C. massiliense var. macroceroides*', and Nel (1968) as '*C. carriense*', '*C. tripos volans*', '*C. tripos volans var. tenuissima*', '*C. macroceras f. armata*', '*C. macroceras var. crassa*', '*C. massiliense f. macroceroides*' and '*C. massiliense f. protuberans*'.

Var. massiliense is a neritic and oceanic warm water taxon, found in all oceans and the Mediterranean. Graham & Bronikowsky (1944) recorded it at an *in situ* temperature range of 10,6–29,5°C in the Pacific and N. Atlantic, where they described it as a tropical taxon, but very tolerant of temperatures below 19°C, most frequent in surface samples, one of the most common taxa of the genus, which could be displaced by ocean currents. In NGY samples, *var. massiliense* was not as common as thus indicated. Specimens with thicker thecal walls and more spinose horns, attributed to *f. armatum* by previous authors, and here treated as belonging to *var. massiliense*, were, in most cases, reported from cooler waters. Karsten's specimens *C. tripos macroceras f. armata* and *C. tripos longipes var. cristata*, provisionally treated as *f. armatum* were found in the S. Atlantic and S. Indian oceans at stations at 40° 31' S., 15° 6,5' E. and 41° 5,8' S., 76° 23,5' E.

Var. carriense has a distribution similar to that of *var. massiliense*, but is rarer. Graham & Bronikowsky found that it did not extend as far outside the tropical regions, and recorded it at an *in situ* temperature range of 12,5–29,5°C.

Ceratiium tenue Ostensfeld & Schmidt (1901): 166, Fig. 18.

Jörgensen (1911): 77, Pl. 9, fig. 163; Mangin (1912): 26, Fig. 11, p.p., (excluding large specimens which are *C. massiliense* (Gour.) Kars.); Pavillard (1916): 18, Pl. 1, Fig. 5; Forti (1922): 74; Steemann Nielsen (1934): 28, Fig. 69; (1939): 15; Nie (1936): 71, Fig. 34; Graham & Bronikowsky (1944): 43.

C. tenue var. buceros (Zach.) Jörgensen (1911): 78, Pl. 9, Figs. 164–166; Forti (1922): 74.

C. tenue f. inclinatum (Kof.) Jörgensen (1911): 78, Pl. 9, Figs. 162, 163.

C. tenue var. inclinatum (Kof.) Graham & Bronikowsky (1944): 43, Fig. 26C.

C. tenue var. tenuissimum (Kof.) Graham & Bronikowsky (1944): 43, Fig. 26D.

- C. buceros f. tenue* (O. & S.) Schiller (1937): 415, Fig. 456a, b (a = Böhm (1931a) Fig. 20, b = Jörgensen (1911) Fig. 163); Rampi (1942): 226, Fig. 9; Gaarder (1954): 10; Wood (1954): 302, Fig. 231a; Halim (1960): 179, Pl. 5, Fig. 16; (1963): 499, Fig. 33; Cassie (1961): 18; Nel (1968); Thornington Smith (1969); Steidinger & Williams (1970): 44, Fig. 12.
- C. buceros var. tenue* (O. & S.) Wood (1963): 5.
- C. buceros tenue*: López (1966): 333, Fig. 41.
- C. horridum subsp. buceros var. tenue* (O. & S.) Jörgensen (1920): 97; Silva (1949): 362; Margalef & Duran (1953): 42, Fig. 12g-i.
- C. horridum var. tenue* (O. & S.) Böhm (1931a): 365, Fig. 20; (1931b): 41.
- ? *C. horridum subsp. tenue*: Dangeard (1927): 379, non Fig. 43a (= *C. trichoceros* (Ehb.) Kof.).
- ? *C. tripos var. horrida* Cleve (1897): 302, Pl. 1, Fig. 4.
- C. horridum* (Cl.) Gran (1902): 194; Ostenfeld (1903): 584; Okamura (1907): 129, p.p., non Pl. 4, Fig. 23 (probably a freak specimen of *C. macroceros* (Ehb.) Cl. as ratio $\frac{B}{H}$ about 1.29); Jörgensen (1920)*: 96; Lebour (1925)*: 155, Pl. 34, Fig. 2; Dangeard (1927)*: 378; Paulsen (1930)*: 91, Fig. 59A-C; Böhm (1931a)*: 365; (1931b)*: 41; Peters (1932)*: 51; Schiller (1937)*: 413, Fig. 455a, b non c (a after Peters, b = Jörgensen (1911) Fig. 176, c, original, = *C. massiliense* as diameter about 70 μ); Silva (1949)*: 362, e.p., (not specimens with diameter $\geq 60 \mu$); Gaarder (1954)*: 12; Wood (1954)*: 300, Fig. 230a, b; (1963)*: 10; Halim (1960)*: 180, Pl. 5, Fig. 10; (1963)*: 499, Fig. 32; Cassie (1961)*: 18, Pl. 7, Fig. 12; López (1966)*: 333, Figs. 42, 43; Taylor (1967)*: 463; Nel (1968); Steidinger & Williams (1970): 46; non Wailes (1928)* Pl. 1, Fig. 1 (= *C. longipes* (Bail.) Gran).
- C. horridum subsp. a horridum*: Jörgensen (1920): 97.
- C. (macroceros subsp.) horridum*: Gran (1902): 193 (in key).
- C. horridum var. horridum*: Graham & Bronikowsky (1944): 42, Figs. 24C 1, 25A-C, G non E, F (= *C. massiliense* on account of size); Sournia (1966): 1982; (1967): 476, Fig. 91; Paredes (1969/70): 43, Pl. 21, Fig. 146.
- C. horridum var. genuina* Gran (1902): 195.
- C. horridum var. genuinum*: Dangeard (1927): 379.
- C. horridum a genuinum*: Jörgensen (1920): 97, Fig. 86.
- C. horridum subsp. horridum var. genuinum*: Jörgensen (1920): 97.
- C. horridum f. genuina* (Gran) Ostenfeld (1903): 585.
- C. horridum f. genuinum*: Peters (1932): 54.
- "*C. horridum* (Cl.) f. *typica* Gran" Ostenfeld (1903): 585, Figs. 136, 137.
- C. horridum f. laevis* Okamura (1907): 129, p.p., Pl. 4, Fig. 21e non d, f h (g).
- C. contortum* (Gour.) Cl., d, f, h = *C. massiliense* on account of size).

* Species cited as *C. horridum* Gran; by Dangeard as *C. horridum* (Gran) Jörg

- C. tripos* β *macroceros* *f. intermedia* Jörgensen (1899): 42, Pl. 1, Fig. 10.
C. horridum var. *intermedia* (Jörg.) Gran (1902): 195.
C. horridum subsp. *horridum* var. *intermedia*: Jörgensen (1920): 97.
C. horridum f. intermedia (Jörg.) Ostenfeld (1903): 585, Fig. 139; Okamura (1907): 129, p.p., Pl. 4, Fig. 21b non a, c (= *C. massiliense* on account of size). "Intermediate between *C. horridum f. typica* and *f. intermedia*": Ostenfeld (1903): 585, Fig. 138.
C. intermedium (Jörg.) Jörgensen (1905): 111; (1911): 83, Pl. 10, Figs. 174–176; Pavillard (1905): 53; (1907): 228; (1931): 91; Paulsen (1907): 22; (1908): 83; Ostenfeld (1931): 615; Wang (1936): 163, Fig. 31; Silva & Pinto (1948): 172, Pl. 2, Fig. 14; ?Wang & Nie (1932): 300, Fig. 13 (diameter given as 60 μ —most likely is *C. massiliense*).
C. intermedium f. spinifera Paulsen (1907): 22; (1908): 83, Fig. 111 (= Ostenfeld (1903) Fig. 136).
C. intermedium f. typica Paulsen (1907): 22; (1908): 83, 84, Fig. 112 (= Ostenfeld (1903) Fig. 139).
C. intermedium f. frigida Paulsen (1907): 22, Fig. 32; (1908): 83, 84, Fig. 113.
C. horridum subsp. *horridum f. frigida* (Pauls.) Jörgensen (1920): 97 (also referred to by Jörgensen (l.c.) as *f. gracilis*).
C. batavum Paulsen (1907): 23, Fig. 33a–d; (1908): 84, Fig. 114.
C. intermedium f. batavum (Pauls.) Jörgensen (1911): 83, 124, Pl. 10, Fig. 177.
C. intermedium var. *batavum* (Pauls.) Ostenfeld (1931): 616.
C. horridum subsp. *horridum* var. *batavum* (Pauls.) Jörgensen (1920): 97.
C. buceros Zacharias (1906): 551, Fig. 15; Schiller (1937): 415; Wood (1954): 301; Cassie (1961): 18; Nel (1968).
C. tripos buceros (Zach.) Karsten (1907): 409, Pl. 48, Fig. 16, non Pl. 51, Fig. 8 (= *C. recurvum* (Jörg.) Reinecke).
C. horridum subsp. *buceros* (Zach.) Jörgensen (1920): 97, Fig. 90; Dangeard (1927): 379.
C. horridum subsp. *buceros f. buceros* (Zach.) Jörgensen (1920): 97; Silva (1949): 362, Pl. 7, Fig. 6.
C. horridum f. buceros: Böhm (1931a): 365.
C. horridum var. *buceros* (Zach.) Sournia (1966): 1982; (1967): 477, Fig. 95.
C. horridum "horridum—*buceros*" Sournia (1966): 1982; (1967): 480, Fig. 92.
C. horridum "horridum > *buceros*" Sournia (1967): 480, Fig. 94.
C. horridum "*buceros* > *horridum*" Sournia (1967): 480, Fig. 93.
C. inclinatum Kofoed (1907b): 303, Pl. 25, figs. 16–21; Pavillard (1931): 91.
C. tripos inclinatum (Kof.) Karsten (1907): 412, 413, Pl. 49, Figs. 19, 20.
C. horridum subsp. *buceros f. inclinatum* (Kof.) Jörgensen (1920): 97, (as a form of subsp. *buceros* var. *tenue*), Fig. 88 (= Jörgensen (1911) Fig. 162a); Silva (1949): 362, Pl. 7, Fig. 5.

- C. horridum f. inclinatum*: Böhm (1931a): 365; (1931b): 41, Fig. 36d, e.
- C. buceros f. inclinatum* (Kof.) Schiller (1937): 415, Fig. 456c (= Jörgensen (1911) Fig. 162a); Rampi (1942): 226, Fig. 16; Gaarder (1954): 10; Wood (1954): 302, Fig. 231b, c; Silva (1956): 22; Halim (1960): 179, Pl. 5, Fig. 17; Taylor (1967): 462; Nel (1968).
- Non C. tripos inclinatum var. minor* Karsten (1907): 412, Pl. 51, Fig. 9a, b (probably = *C. declinatum* Kars.).
- C. mollis* Kofoed (1907b): 304, Pl. 27, Fig. 29.
- C. molle* Kof.: Jörgensen (1911): 81, Pl. 9, Fig. 170, Pl. 10, Figs. 171, 172; Schröder (1911): 647; Pavillard (1916): 19; (1931): 90; Forti (1922): 75; Steemann Nielsen (1934): 28, Fig. 71; (1939): 15; Wang (1936): 162, Fig. 30.
- C. horridum subsp. buceros var. molle* (Kof.) Jörgensen (1920): 97, Fig. 87; *non* Margalef & Duran (1953): 42, Fig. 12j, k (= *C. massiliense* on account of size).
- C. horridum subsp. buceros var. molle*: Silva (1949): 362, Pl. 7, Fig. 7, Pl. 9, Fig. 13.
- C. horridum var. molle*: Böhm (1931a): 365; (1931b): 41, Fig. 36a-c; Graham & Bronikowsky (1944): 42, Figs. 231, K, 25D.
- C. buceros f. molle* (Kof.) Schiller (1937): 417, Fig. 457a (= Jörgensen (1911) Fig. 170); Rampi (1942): 226, Fig. 17; Gaarder (1954): 10; Wood (1954): 303, Fig. 231g; Silva (1956): 22; Halim (1960) Pl. 5, fig. 13; Cassie (1961): 18, Pl. 7, Fig. 14.
- C. buceros var. molle* (Kof.) Wood (1963): 5.
- C. buceros molle*: López (1966): 333, Fig. 39, 40.
- C. tenuissimum* Kofoed (1907b): 307, Pl. 29, Figs. 32, 33; Paulsen (1930): 93, Fig. 60A, B.
- C. tripos volans var. tenuissima* (Kof.) Karsten (1907): 409, Pl. 49, Fig. 17a *non* b (= *C. massiliense var. carriense* (Gour.) Reinecke, on account of size).
- C. horridum subsp. buceros f. tenuissimum* (Kof.) Jörgensen (1920): 97, Fig. 89 (= Jörgensen (1911) Fig. 166 under *C. tenue var. buceros*).
- C. horridum f. tenuissimum* (Kof.) Böhm (1931a): 365.
- C. buceros f. tenuissimum* (Kof.) Schiller (1937): 417, Fig. 457a (= Jörgensen (1911) Fig. 166); Rampi (1942): 227, Fig. 18; Gaarder (1954): 10; Wood (1954): 303, Fig. 231h; Halim (1963): 499, Fig. 34.
- Non C. tripos macroceras var. tenuissima n. var.* Karsten (1907): 411, Pl. 49, Fig. 28 (= *C. macroceras*).
- C. horridum subsp. buceros var. denticulatum* Jörgensen (1920): 97, Fig. 91.
- C. horridum subsp. buceros f. denticulatum* (Jörg.) Silva (1949): 352, Pl. 7, Fig. 8.
- C. denticulatum* (Jörg.) Paulsen (1930): 93, Fig. 61.
- C. horridum f. denticulatum* (Jörg.) Böhm (1931a): 365; (1931b): 41, Fig. 36f, g.
- C. buceros f. denticulatum* (Jörg.) Schiller (1937): 417, Fig. 457b (= Paulsen (1930) Fig. 61); Rampi (1942): 227, Fig. 15; Wood (1954): 303, Fig. 231i; Halim (1960): 179; Cassie (1961): 18; Nel (1968); Thornington Smith (1969).

C. claviger Kofoid (1907a): 170, Pl. 4, Fig. 27; Jörgensen (1911): 80, Pl. 9, Figs. 168, 169; Pavillard (1916): 18, Pl. 1, Fig. 6 (queried by him, as tips of antapical horns not shown); Steemann Nielsen (1934): 28, Fig. 70.

C. horridum subsp. buceros f. claviger (Kof.) Jörgensen (1920): 97 (suggested by him as a form of *subsp. buceros var. molle*).

C. horridum subsp. claviger (Kof.) Dangeard (1927): 379.

C. horridum var. claviger (Kof.) Graham & Bronikowsky (1944): 42, Fig. 23J, L.

C. horridum f. claviger (Kof.) Sournia (1967): 480.

C. buceros f. claviger (Kof.) Schiller (1937): 415, Fig. 456e (= Jörgensen (1911) Fig. 168); Rampi (1942): 226, Fig. 13; Wood (1954): 303, Fig. 231e, f; Silva (1955): 171, Pl. 9, Fig. 4; Halim (1960) Pl. 5, Fig. 12; Nel (1968).

C. leptosomum: Dangeard (1927): 379, Fig. 43c.

C. buceros f. leptosomum: Rampi (1942): 226, Fig. 19; Wood (1954): 302, Fig. 231d; ?Taylor (1967): 462; *non* Schiller (1937): 415, Fig. 456d (= Jörgensen (1911) Fig. 67).

Non C. leptosomum Jörgensen (1911): 80, Pl. 9, Fig. 167 (most like *C. macroceros*, ratio $\frac{B}{H}$ about 1.06).

? "*C. horridum subsp. buceros*, a degenerate form answering to *f. californiense* of *C. macroceros subsp. gallicum*": Jörgensen (1920): 98, Fig. 92 (= heteromorphic short horned specimen of uncertain affinity).

C. volans: Okamura (1907): 130, e.p., Pl. 4, Fig. 18a *non* b-e (= *C. massiliense* on account of size); *non C. (tripos var. ?) volans* Cleve.

C. carriense var. volans: Silva (1955): 172, e.p., Pl. 9, Fig. 5 (specimen with small diameter).

C. massiliense: Peters (1932) e.p., Pl. 4, Fig. 17f.

C. tripos volans f. recurvata Karsten (1906): 144, Pl. 21, Fig. 22.

C. tripos flagelliferum f. angusta Karsten (1906): 146, e.p., Pl. 22, Fig. 33b *non* a (= *C. trichoceros*).

C. tripos flagelliferum var. angusta Karsten (1907): 410, 411, e.p., Pl. 49, Fig. 24b *non* a, c (a = *C. trichoceros*, b = *C. massiliense* on account of size).

? *C. flagelliferum var. filiformis* Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 11.

C. tripos patentissimum: Karsten (1906): 144, Pl. 21, Fig. 23, *non C. patentissimum* O. & S.

C. tripos inversum Karsten (1907): 539 (= *C. tripos patentissimum* Karsten 1906).

? *C. tripos scoticum* Schütt (1892): 308, e.p., Fig. 91 IV *non*: 266, Fig. 76 IVc (= *C. macroceros*).

C. macroceras var. scotica (Schütt) Ostenfeld & Schmidt (1901): 167.

C. tripos macroceros f. undulata Schröder (1900): 16, e.p., Pl. 1, Fig. 17l *non* k, m (k = *C. massiliense*, m = *C. vultur var. pavillardii* (Jörg.) Reinecke).

C. macroceros: Lebour (1925): 155, e.p., Pl. 35, Fig. 1.

C. tripos macroceras f. graciosa Stüwe (1909): 274, Pl. 1, Fig. 9.

C. tripos sufflatum Stüwe (1909): 274, Pl. 1, Fig. 11.

Diagnosis: In the specimens examined, *C. tenue* differs from *C. massiliense* (Gour.) Kars. in that the girdle diameter is $< 60 \mu$; *C. tenue* differs from *C. deflexum* (Kof.) Jörg. in that the right horn degree co-ordinate with the 15μ radius co-ordinate is $> 45^\circ$; *C. tenue* differs from *C. trichoceros* (Ehb.) Kof. in that the left horn MRC occurs before the 75μ radius co-ordinate; (the single specimen of *C. tenue* in which the left horn MRC occurred beyond the 75μ radius co-ordinate, differed from *C. trichoceros* in that the left horn degree co-ordinate with the 15μ radius co-ordinate was $> 90^\circ$ and the right horn MRC occurred before the 60μ radius co-ordinate); *C. tenue* differs from *C. macroceros* (Ehb.) C. & L. in that the ratio $\frac{B}{H}$ is < 0.60 .

Taxonomic history and present-treatment: *C. tenue* is the most variable species of *Ceratium*, and, as the synonymy shows, has had an extremely diverse taxonomic treatment. Jörgensen (1920) was the first to group its variants together in a single species "*C. horridum* Gran", consisting of two subspecies and a number of varieties and forms: *subsp. horridum* (also referred to by him as *a. genuinum* Gran), with the infra-subspecific taxa *var. genuinum* Gran, *var. intermedium* (Jörg.), *var. batavum* (Pauls.) and *f. frigida* (Pauls.) and *subsp. buceros* (Zach.) with the infra-subspecific taxa *var. molle* (Kof.), *var. tenue* (O. & S.), *Var. denticulatum* Jörg., *f. inclinatum* (Kof.), *f. tenuissimum* (Kof.), *f. claviger* (Kof.) and *f. buceros*. This procedure was not universally adopted. Schiller (1937), for example, referred to "*C. horridum* Gran" and *C. buceros* Zach., the latter consisting of *f. tenue* (O. & S.) Jörg., *f. inclinatum* (Kof.) Jörg., *f. leptosomum* (Jörg.) Sch., *f. claviger* (Kof.) Jörg., *f. molle* (Kof.) Jörg., *f. tenuissimum* (Kof.) Jörg. and *f. denticulatum* (Jörg.) Sch. Sournia (1966, 1967) proposed a new treatment "outside the classical taxonomy", reducing the "*C. horridum*" complex to one species with three infraspecific taxa, *C. horridum var. horridum* (Cl.) Gran, *var. buceros* (Zach.) Sour. and *f. claviger* (Kof.) Sour. Intermediates between *var. horridum* and *var. buceros* were referred to as "*horridum—buceros*" "*horridum > buceros*" or "*buceros > horridum*".

An examination of the range of variation in specimens of *C. tenue* in the Agulhas current showed that it was quite impossible to delimit any infraspecific groups. An apparent discontinuity was found in the polar co-ordinate measurements of the curvature of the right horn, in that the degree co-ordinate with the 150μ radius co-ordinate was $< 120^\circ$ or $> 125^\circ$, (see Fig. 17B). However, in more than half the specimens, the right horn did not extend to the 150μ radius co-ordinate, and when the degree co-ordinate for this point was estimated in these, the discontinuity was eliminated. In some specimens, measurements of antapical horn curvature was further complicated by horn flexibility. (In three specimens of *C. tenue* seen from Oslo Fiord, the right horn degree co-ordinate

with the 150 μ radius co-ordinate was estimated at between 120 and 130°). See Figs 18–20.

When treated as a single variable species, this species has always been referred to as "*C. horridum* (Cl.) Gran" or "*C. horridum* Gran". This is incorrect, for, following Article 60 of the International Code, which states that "In no case does a name or an epithet have priority outside its own rank", the species must be known as *C. tenue* Ostenfeld & Schmidt. This is fortunate, for the name "*C. tripos* var. *horrida* Cleve" might be regarded as a *nomen confusum*.

Cleve (1897) wrote of his new taxon *C. tripos* var. *horrida*: "... resembles the var. *longipes*, but is remarkable for the spines on the horns and the tail...". In 1900, in the synonymy of "*C. tripos longipes* Bail.", Cleve (1900b), wrote: "... inclusive var. *horrida* Cl. l.c. Fig. 4..." referring to his iconotype of *C. tripos* var. *horrida*. Jørgensen (1905) also considered that Cleve's iconotype represented *C. longipes* (Bail.) Gran, writing: "Cleve's figure... clearly shows the curved horn which is typical for *C. longipes*...". He maintained this view in 1911, commenting that this figure belonged to those illustrations of Cleve "which in themselves are impossible to interpret and consequently have only brought uncertainty and confusion". In 1920, he referred to "*C. horridum*

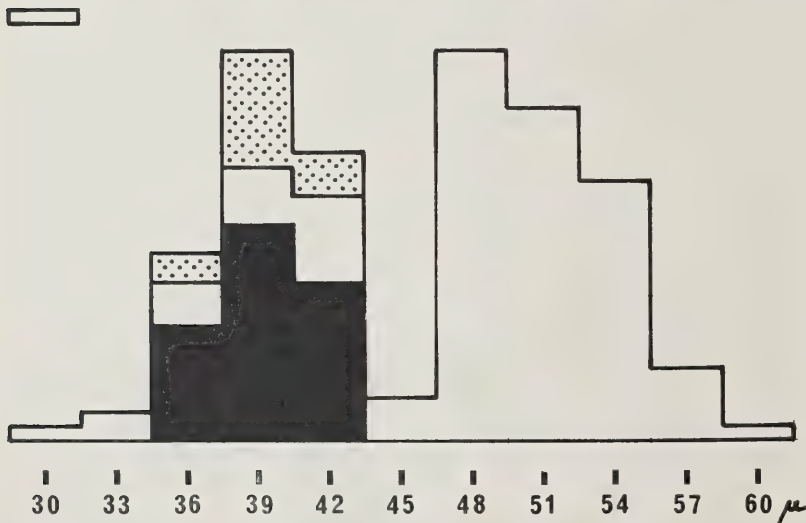


FIG. 21.

C. trichoceros (Ehb.) Kof.: Variation in girdle diameter in specimens from Agulhas current NGY samples. Black shading = presence of "basal kink" in left horn, white shading = absence of this kink, dotted shading = nature of base of left horn not recorded; single bar indicates one specimen.

Gran", noting that Cleve's figure of *C. tripos* var. *horrida* "may be this species, but is at least as likely to represent *C. longipes* var. *oceanicum* Ostf." Most authors after Jörgensen cited the taxon as "*C. horridum* Gran"; both Schiller (1937) and Wood (1954) writing in the synonymy: "*vix C. tripos* var. *horrida* Cleve".

C. batavum Paulsen is included in the synonymy of *C. tenue*, but the specimen of Figure 33b accompanying Paulsen's type description (1907), has a slightly curved apical horn.* A numerical assessment, using polar co-ordinate measurements of apical and antapical horn curvature, of the differences between *C. tenue*, *C. longipes* and *C. arcticum* (Ehb.) Cl. would be extremely useful. The last two species were not recorded from the Agulhas current samples. Graham & Bronikowsky (1944) combined *C. longipes* and *C. arcticum* into one species, *C. arcticum*.

The range of variation in antapical horn curvature in *C. tenue* is paralleled in *C. massiliense*. Size is the main criterion for the separation of the two species, for actual antapical horn curvature is very similar. (See Fig. 10.) In the Agulhas current samples, the girdle diameter in *C. tenue* was $\leq 54 \mu$ and in *C. massiliense* $\geq 60 \mu$, so that the species were always easily recognisable. A number of authors give girdle diameters for *C. tenue* in excess of 60μ , and these are treated here as pertaining to *C. massiliense*. In general, specimens of *C. tenue* with spreading antapical horns and thin-walled thecae have a diameter of less than 50μ (eg. Kofoid (1907b) gives diameters of $35\text{--}45 \mu$ and $32\text{--}42 \mu$ for *C. tenuissimum* and *C. inclinatum*), while in those with less spreading horns and thick thecal walls, diameters in excess of 50μ are recorded (eg. Jörgensen (1911) gives a diameter of $42\text{--}57 \mu$ for *C. intermedium*).

The problem of the taxon *C. massiliense* f. *armatum* (Kars.) Jörg. has been mentioned. In Karsten's figures (1905, Pl. 19, Figs. 7, 8), the spines supporting lists along the lower edge of the antapical horns, are prominent beyond the level of the base of the apical horn, as is usually the case in specimens of *C. tenue* with spiny antapical lists, and not otherwise the case in *C. massiliense*. Karsten himself later (1906) considered his specimen to belong to *C. horridum*, but its diameter, calculated from the scale of the figure, is in excess of 65μ .

Variation in thecal ornamentation, horn curvature and relative length: The apical horn is straight or very slightly curved. The antapical horns, after the forward recurvature, vary from being extremely spreading, lying roughly at right angles to the apical horn, to lying parallel to it. Entire antapical horns with closed tapered tips, vary in length, from extending to a level about half the length of the body along the apical horn, to extending to roughly the length of the apical

* Ostenfeld (1931) commented on '*C. intermedium* var. *batavum*': "... perhaps more likely belongs to *C. longipes*."

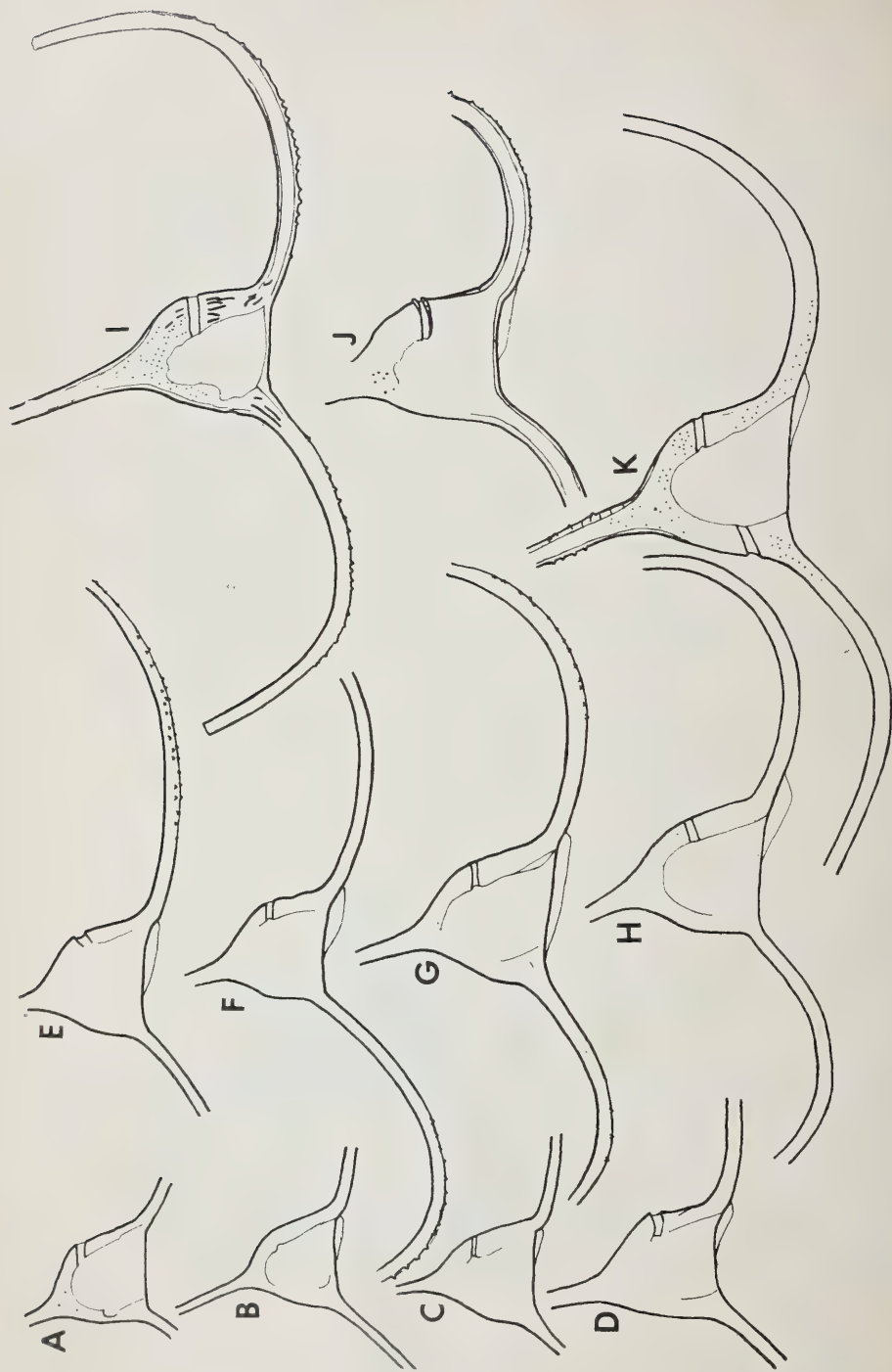


FIG. 22.

A-F, *C. trichoceros* var. *trichoceros* (Ehb.) Kof.; G-K, *C. trichoceros* var. *contrarium* (Gour.) Sch.: Obvious left horn "basal kink" in B, C and E, slight kink in D; girdle incomplete in all save K; unusually thickened basal wall in I and J from station NGY 41 (see page 71); thecal wall in optical section and surface view in H, I, J, K; measurements of the current NGY stations. Girdle diameters: A 39 μ , B 36 μ , C 39 μ , D 42 μ , E 42 μ , F 42 μ , G 51 μ , H 48 μ , I 48 μ , J 48 μ , K 57 μ .

horn. A list of varying width is almost always present between the base of the hypotheca and the base of the left horn, extending a varying distance along the base of the hypotheca, sometimes as far as the right side of the sulcus, and to the point of MBC on the horn, where it may be supported by a single spine.

A linear series of variations is found, with the short antapical-horned specimens in the middle. These generally have thin thecae and spineless horns, or a few minute spines along the lower margins of the antapical horns in the region of recurvature, and correspond approximately to the original concept of *C. tenue* O. & S. On the one side of the series of variations, the antapical horns become thicker proximally, longer, but never the full length of the apical horn, and less spreading to roughly parallel to the apical horn. The thecal wall may become thicker and ridged, with spines along the proximal part of the apical horn, sometimes in four rows along the plate sutures, and along the lower margins of the antapical horns. On the antapical horns, the spines vary from small denticles to prominent spines supporting lists, when the spines usually extend along the horns beyond the level of the base of the apical horn, gradually decreasing in size distally and lists may occur right across the base of the hypotheca; generally the longer the spines, the less the difference in their length at the base of the horn and at the level of the base of the apical horn. Similarly, the apical horn spines on the right and left sides may be very prominent, supporting lists, and extending along the horn for at least half its length.

The heaviest spines tend to be found in specimens in which the antapical horns are not very spreading, but not always. In specimens corresponding to *C. intermedium* f. *frigida* Pauls. for example, the horns are parallel to the apical horn, proximally stout and smooth, save for a few denticles on the left horn in the region of recurvature. Specimens are found either with the antapical horns broken, or with closed tapered ends; according to Nie (1936) "often with an obscure terminal pore". Sometimes, particularly noticeable in very thick-walled specimens, the distal parts of the antapical horns are thin-walled, more slender and flexible, often with the tips inflated, sometimes markedly so. This side of the linear series of variations may be described in terms of previously described taxa thus: *C. tenue* → *C. batavum* Pauls. → *C. tripos* β *macroceros* f. *intermedia* Jörg. → "*C. horridum* f. *typica* Gran" Ost. with *C. intermedia* f. *frigida* representing specimens with close antapical horns without heavy spines. It is specimens exhibiting the above range of variation which are found in colder waters. (See Figs. 18H, 19 and 20.)

On the other side of the linear series of variations, the antapical horns remain thin and increase markedly in length, becoming either very spreading, distally sometimes recurving outwards or inwards, or, more rarely, lying parallel to the apical horn. The distal parts of the antapical horns are flexible, the horn tips tapered-rounded and closed, sometimes slightly inflated. The thecal wall is

generally thin, the horns smooth or with minute spines, sometimes supporting a narrow list along the region of recurvature of the antapical horns. In terms of previously described taxa, the linear series of variations is described thus: *C. tenue* → *C. inclinatum* Kof. → *C. buceros* Zach., *C. horridum* subsp. *buceros* var. *denticulatum* Jörg. and *C. tenuissimum* Kof., with *C. molle* Kof. representing the thin-horned specimens in which the antapical horns lie parallel to the apical horn. These forms are confined to warmer waters. (See Fig. 18 A–G.)

There is no discontinuity in this series of variations and further, specimens are found with smooth antapical horns more or less parallel to the apical horn, which are of an intermediate thickness, represented by *C. claviger* Kof., the first specimen figured with clavate horn tips, in this case, bifid in the right horn. (See Fig. 19 D.)

Polar co-ordinate measurements of antapical horn curvature: In some instances, distal parts of horns flexible, sometimes curved outwards; horns extend to 150 μ radius in less than half specimens examined. *Left horn:* MBC co-ordinates 65–90° and 0–15 μ ; degree co-ordinate with 15 μ radius co-ordinate 70–110°, with 105 μ , 114–194°, with 195 μ , 109–203°; MRC occurs mostly between 15 and 30 μ radius co-ordinates, very rarely beyond up to between 75 and 90 μ co-ordinates and is 11–30°; $\frac{L^{90}}{D}$ 0,00–0,77, mostly < 0,60; $\frac{B}{H}$ 0,03–0,56, mostly 0,10–0,40. *Right horn:* MBC co-ordinates 59–85° and 3–33 μ ; degree co-ordinate with 15 μ radius co-ordinate 50–100°, with 105 μ , 85–146°, with 150 μ , 83–147°, with 195 μ , 82–147°; MRC occurs between 15 and 60 μ radius co-ordinates, mostly between 15 and 30 μ and is 8–23°; $\frac{R^{90}}{D}$ 0,13–1,25, mostly 0,40–0,80, occasionally horn so spreading that 90° co-ordinate not reached. (See Fig. 17.)

Dimensions: In specimens examined: Girdle diameter 30–54 μ (48–54 μ in three specimens seen from Oslo Fiord); length body 33–60 μ ; length hypotheca 15–33 μ ; length epitheca 12–30 μ ; length apical horn 96–735 μ . *From literature:* Diameter: 32–45 μ (Kofoid (1907)); 36–57 μ (Jørgensen 1911); 42–47 μ (Lebour 1925); 35–37 μ (Nie 1936); 32–43 μ (Steemann Nielsen 1934); average diameter of “*C. horridum*” 44 μ , of *C. tenue* 37 μ (Graham & Bronikowsky 1944); average diameter of “*C. molle*” 40 μ , of “*C. intermedium*” 58 μ (Wang 1936, probably including specimens of *C. massiliense*); length apical horn 150–450 μ (Jørgensen 1911).

Distribution: *C. tenue* is found in all oceans and the Mediterranean. The forms with thin horns on the one side of the line of variations are confined to warmer waters, while the forms with thicker horns have a very wide temperature tolerance and are cosmopolitan. However, the development of heavy spines along the horns appears to be associated with cooler waters, for there are no illustrated records of specimens of *C. tenue* with prominent spines from the tropics. Graham & Bronikowsky found both *C. tenue* and “*C. horridum*” to be shade species.

The distribution of *C. tenue* in the Agulhas current NGY stations is shown in Tables 1 and 2. In the Port Elizabeth line of stations, a wide range of variation was generally found at each station, but specimens with heavy spines were not common, except at the May cruise station 41, immediately off Port Elizabeth, where a number of specimens were seen with thick horns and thecal walls, generally with prominent spines supporting lists along the horns, such as in specimens from the Faeroes depicted by Ostenfeld (1903). Upwelling occurs off Port Elizabeth, and there is a North flowing current inshore of the Agulhas current, which originates in the vicinity of Cape Agulhas. It is more probable that these heavily spined forms developed as the result of an upwelling.

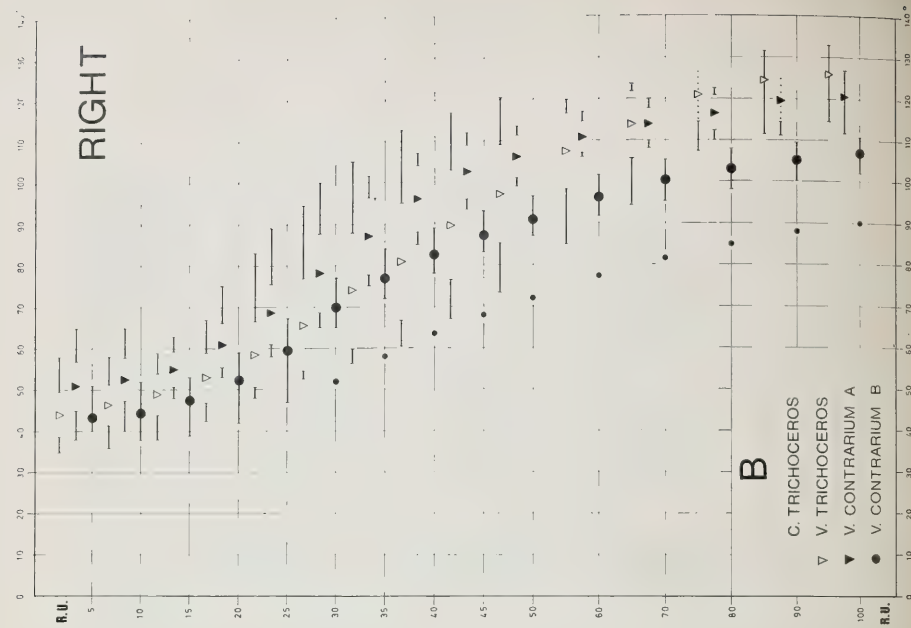
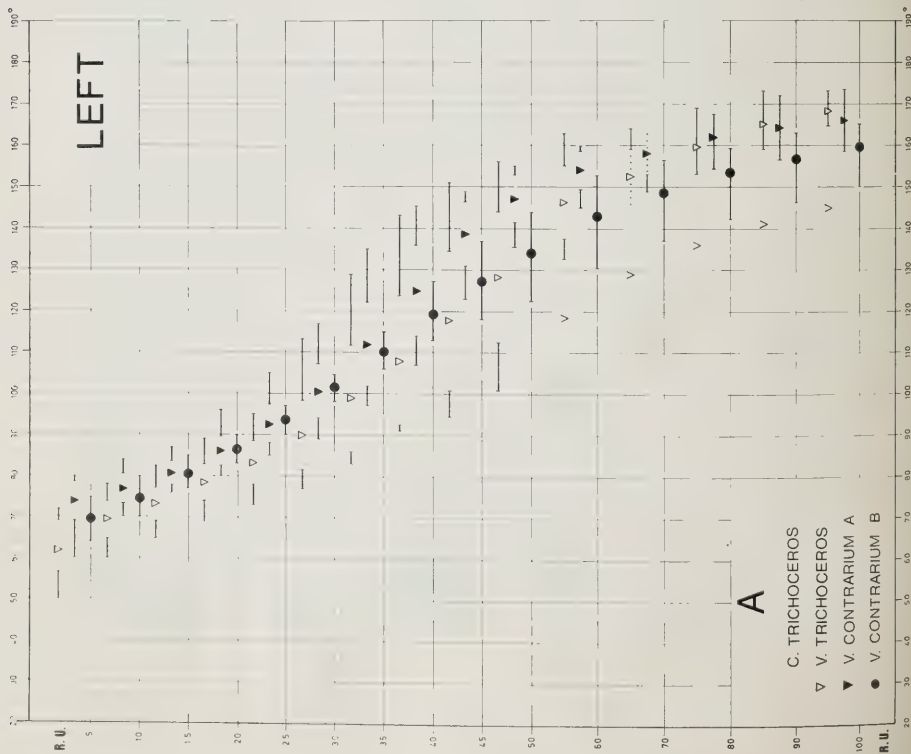
Cultur experiments on the effects of temperature on the different forms would be helpful in determining the exact nature of this variation.

Ceratium trichoceros (Ehrenberg) Kofoid (1908a): 362, Figs. 16-19.

Diagnosis: *C. trichoceros* is characterised by the fact that the left horn MRC occurs beyond the $75\ \mu$ radius co-ordinate. It differs from those specimens of other species of Subsection *Macroceras* in which the left horn MRC occurs beyond the $75\ \mu$ radius co-ordinate thus: from *C. macroceras* (Ehb.) Vanh. in that the left horn MBC degree co-ordinate is generally $\geq 70^\circ$; the few specimens of *C. trichoceros* in which this co-ordinate is $< 70^\circ$, but $\geq 65^\circ$, differ from the few specimens of *C. macroceras* in which this co-ordinate is $\geq 65^\circ$, in that the girdle diameter is $\leq 45\ \mu$, while in the specimens of *C. macroceras* it is $\geq 55\ \mu$; from the single specimen of *C. massiliense* var. *massiliense* (Gou.) Kars. recorded, in that the left horn degree co-ordinate with the $15\ \mu$ radius co-ordinate is $> 90^\circ$, and from the single specimen of *C. massiliense* var. *carriense* (Gour.) Rein. recorded, in that in specimens with a girdle diameter $> 45\ \mu$, the left horn MBC degree co-ordinate is $\geq 70^\circ$; from the single specimen of *C. tenue* O. & S. recorded in that the left horn degree co-ordinate with the $15\ \mu$ radius co-ordinate is $< 90^\circ$; from *C. deflexum* f. *sinensis* Rein. in that the right horn MBC degree co-ordinate is $> 40^\circ$.

Taxonomic history and present treatment: The two varieties of *C. trichoceros*, var. *trichoceros* and var. *contrarium* (Gour.) Sch. were first combined into one species by Schiller (1937), although the evidence suggests that earlier authors, in particular Cleve (1900a, b), had treated elements of both as belonging to a single taxon. Schiller's treatment was not universally adopted.

Sournia (1967) considered that the differences between the two were quite sufficient for their retention as separate species. The differences he listed, following Jörgensen (1911), were: in *C. contrarium* (Gour.) Pav., in comparison with *C. trichoceros*, the central body was larger, the left profile of the hypotheca more oblique and slightly concave, the epitheca was broader than high and the



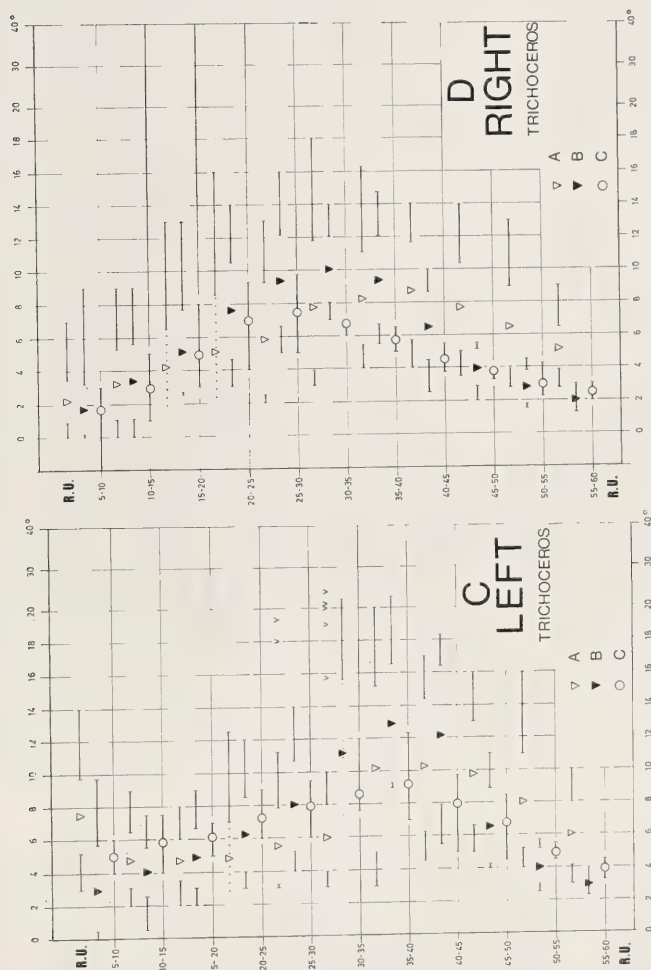


FIG. 23A-D.
C. trichoceros (Ehb.) Kof.: Antapical horn curvature in specimens from Agulhas current NGY stations. A, curvature of left horn expressed in degrees at 5 R.U. intervals from 5 to 50 R.U. and at 10 R.U. intervals from 50 to 100 R.U.; B, the same for the right horn; C, the rate of change of direction of curvature of the left horn expressed in degrees over 5 R.U. from 5-10 to 55-60 R.U.; A = *var. trichoceros*, B = *var. contrarium* (Gourret) Schiller A, C = *var. contrarium* B; D, the same for the right horn. In *var. contrarium* B the right horn is more spreading than in *var. contrarium* A. See Key to Fig. 5 and page 81.

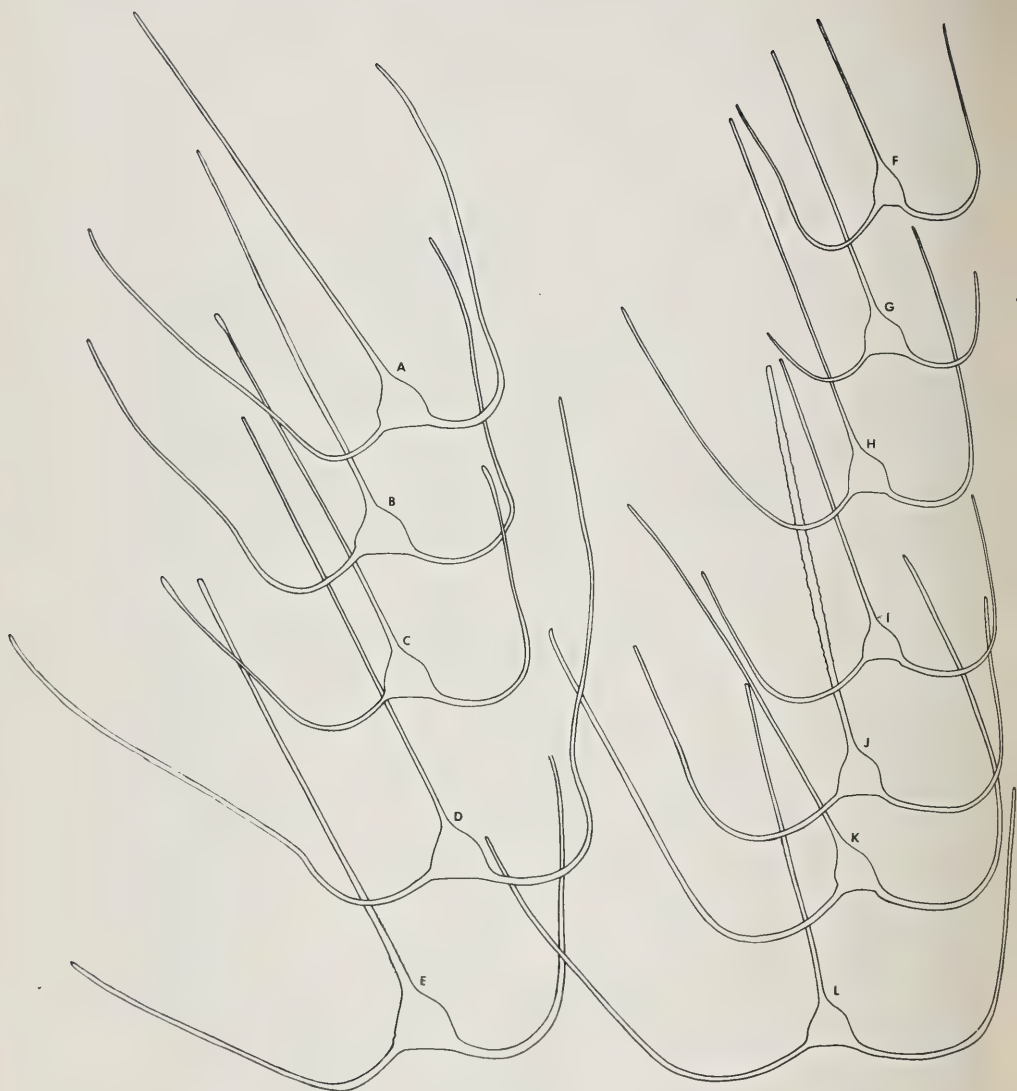


FIG. 24.

A-E, *C. trichoceros* var. *contrarium* (Gour.) Sch., F-L, *C. trichoceros* var. *trichoceros* (Ehb.) Kof.: Showing variation in antapical horn curvature; basal "kink" present in left horn of I and K; tips of antapical and apical horns inflated in C; apical horn inflated, with rows of spines along plate sutures in J; E, specimen with complete girdle and divergent antapical horns; girdle incomplete in others. All specimens from Agulhas current NGY stations. Girdle diameter: A 45 μ , B 48 μ , C 48 μ , D 54 μ , E 57 μ , F 30 μ , G 42 μ , H 39 μ , I 36 μ , J 42 μ , K 36 μ , L 39 μ .

girdle normally developed; the base of the left antapical horn was nearly continuous with the base of the hypotheca and lacked a basal "kink"; the recurvature of the right horn occurred about one or less than one girdle diameter along the horn, (in *C. trichoceros* about one to two girdle diameters); the antapical horns were not symmetrically curved, the right being more abruptly recurved and this recurvature occurring more anteriorly than in the left horn. Further there were some differences in the distribution of the two species.

A study of specimens depicted in the literature and from the Agulhas current NGY samples, indicates that, while two taxa can be identified, their separation into distinct species is not justified. The points of difference listed by Sournia are discussed below.

Examination of the girdle diameter in 140 NGY specimens, measured correct to 3 μ , showed a discontinuity in the measurements indicating two groups: the first with a diameter of 30–42 μ , the second with a diameter of 48–60 μ ; in only three specimens was the diameter 45 μ . (Jørgensen (1911) gave the diameter of *C. trichoceros* as 37–48 μ and of '*C. inflexum* (Gour.) Kof.' (= *var. contrarium*) as 51–68 μ .) See Fig. 21.

Body shape varied regardless of size in both NGY specimens and those figured in the literature, and in all 75 NGY specimens measured, (and in Ehrenberg's iconotype), the width of the epitheca exceeded its height.

With regard to development of the girdle, it was sometimes incompletely developed in NGY specimens with a diameter exceeding 50 μ . When development of the girdle is incomplete, seen dorsally, the girdle lists are fully developed on the left side, becoming less developed to almost non-existent on the right. Seen ventrally, the girdle is fully developed on the left side of the sulcus, and completely absent or very faintly developed on the right. Sometimes the girdle lists are so slightly developed and the thecal wall is so thin, that the girdle is almost invisible at low magnification. It is often difficult to judge the nature of the girdle in figures from the literature. For example, in both Ehrenberg's iconotype and Cleve's figure (1900a) of "*C. flagelliferum*" the specimens are drawn seen ventrally, but the girdle is shown in dorsal aspect, extending right across the cell.

The basal "kink" of the left horn refers to a slight kink of the lower posterior edge of the horn about 3 μ from its origin adjacent to the hypotheca, the angle of the kink projecting outwards. In 16/50 NGY specimens with a diameter $\approx$ 42 μ , this kink was absent. It was never observed in NGY specimens with a diameter $\geq$ 45 μ . In all NGY specimens with this kink, the lower posterior edge of the left horn is markedly delimited from the hypotheca base, making an obvious angle with it. When the "kink" is absent, the delimitation of the base of the left horn from the base of the hypotheca is less marked to almost imperceptible. Generally, the larger the girdle diameter, the less apparent is this delimitation.

but NGY specimens with diameters of 42 μ and 51 μ were seen in which the angular delimitation between the base of the left horn and the hypotheca was virtually the same. (See Fig. 22.)

A comparison of the curvature of the right and left horns in NGY specimens using polar co-ordinates, showed that in the right horn, the MRC occurred at the same or at a shorter distance along the horn than the left horn MRC; only in one small diametered specimen did the MRC occur further along the right horn than the left, (also in Ehrenberg's iconotype). The situation of the MRC at a shorter distance along the right horn than along the left was more frequent in larger specimens. The ratio $\frac{RMBC}{D}$ never exceeded 1,75 in specimens with a diameter $\geq 45 \mu$. In the smaller specimens, this ratio was as large as 3,81, but individuals with low ratios were also found (eg. diameter 42 μ , $\frac{RMBC}{D}$ 1,27, diameter 39 μ , $\frac{RMBC}{D}$ 1,54). See Table 5.

It is clear that the above characters do indicate the existence of two taxa, but are insufficiently different in the two groups to warrant the establishment of two distinct species.

Description: Base of right horn always delimited from base of hypotheca, making a sharp or a rounded angle with it. Base of left horn in *var. trichoceros* generally makes an obvious angle with the base of the hypotheca and often has a slight "kink" about 3 μ from it; in *var. contrarium*, base of left horn mostly not markedly delimited from base of hypotheca.

Antapical horn curvature: Initially, proximal parts of horns very spreading; polar co-ordinate measurements of horn curvature in specimens examined: Left horn: degree co-ordinate with 15 μ radius co-ordinate 50–80°, generally < 70° in *var. trichoceros* and > 70° in *var. contrarium*; MBC degree co-ordinates 65–85°, (< 70° recorded in only three specimens), mostly 72–78° in *var. trichoceros* and 75–82° in *var. contrarium*; MBC radius co-ordinate 22–75 μ , (95 μ recorded in one specimen), mostly 40–62 μ in *var. trichoceros* and 34–42 μ in *var. contrarium*. After initial change from zero point to 15 μ radius co-ordinate, two patterns of horn curvature are found: in the first, there is a gradual increase in rate of change of direction over successive 15 μ intervals up to zone of MRC; in the second, rate of change over 15 μ decreases beyond the 30 μ radius co-ordinate and then increases to a rate exceeding that between the 15 and 30 μ radius co-ordinates, up to zone of MRC; second pattern usually found in *var. trichoceros*, first in *var. contrarium*. MRC occurs beyond 75 μ radius co-ordinate, up to between 150 and 165 μ radius co-ordinates in *var. trichoceros*, generally not beyond 120 μ in *var. contrarium*, and is 8–25°, mostly 10–20°; degree co-ordinate with 150 μ radius co-ordinate very variable, 93–156° in *var. trichoceros*, 123–155° in *var. contrarium*; with 300 μ , values from 144–175° recorded in the few specimens seen with left horn extending to this level. *Right*

horn: degree co-ordinate with $15\ \mu$ radius co-ordinate $25-60^\circ$, less than in left horn by up to 35° ; curvature mostly of first type described above; MBC degree co-ordinate $50-70^\circ$, less than in left horn by up to 27° , mostly by $6-20^\circ$; MBC radius co-ordinates $37-120\ \mu$ ($153\ \mu$ recorded in one specimen) greater than in left horn by up to $60\ \mu$ (by $101\ \mu$ in one specimen), (less than in left horn in one specimen), mostly $67-105\ \mu$ in *var. trichoceros* and $57-78\ \mu$ in *var. contrarium*; MRC occurs at same distance along right horn as along left, or at shorter distance, rarely further along horn; occurrence of MRC at shorter distance along right horn than along left more common in *var. contrarium*; degree co-ordinate with $150\ \mu$ radius co-ordinate $72-121^\circ$; with $300\ \mu$, $90-135^\circ$ in few specimens recorded ($< 100^\circ$ in a single specimen). See Fig. 23.

Beyond zone of MRC, rate of change of direction of curvature over successive $15\ \mu$ intervals decreases and right and left horns tend to lie roughly parallel to one another and apical horn; wall of distal parts of antapical horns tends to be thinner and distal parts may be slightly undulating, the latter often the case in *var. contrarium*, rarely in *var. trichoceros*. (See Fig. 24.)

Spreading nature of proximal parts of antapical horns may be measured by radius co-ordinate with 90° co-ordinate: L90 $45-135\ \mu$, mostly $80-110\ \mu$ in *var. trichoceros*, mostly $60-80\ \mu$ in *var. contrarium*; R90 $75-221\ \mu$, mostly $105-115\ \mu$ in *var. trichoceros*, mostly $90-125\ \mu$ in *var. contrarium*; $\frac{L90}{D}$ $0.94-3.17$, mostly $1.80-2.85$ in *var. trichoceros*, mostly $1.15-1.80$ in *var. contrarium*; $\frac{R90}{D}$ $1.78-5.95$, mostly $2.50-4.00$ in *var. trichoceros*, mostly $1.90-2.50$ in *var. contrarium*; ratio $\frac{B}{H}$ difficult to calculate because of incomplete formation of girdle, varies from $0.40-2.80$ in specimens measured, is usually higher in *var. trichoceros* than in *var. contrarium*.

Thecal ornamentation: Variation in girdle development has been discussed; thecal wall generally thin; smooth margined list usually present between base of hypotheca and left horn; minute spines sometimes present along lower edge of proximal parts of antapical horns in *var. trichoceros*, very rarely in *var. contrarium*, (Karsten (1906) Pl. 22, fig. 32b, shows spines along upper edges of antapical horns as well); minute spines may be present on either side of proximal part of apical horn. In *var. contrarium*, tips of antapical horns occasionally clavate to a varying degree, this inflation sometimes retuse; inflated tips apparently not recorded for *var. trichoceros*; apical horn sometimes inflated for almost entire length and ornamented with minute spines, mostly found in *var. trichoceros*; in specimens of *var. contrarium* with inflated antapical horn tips, tip of apical horn sometimes inflated. Some specimens of *var. contrarium* with markedly thickened thecal walls and incompletely formed girdles were seen in the Agulhas current NGY station 41 immediately off Port Elizabeth. (Refer to account of distribution of *C. tenue*.)

In the Agulhas current NGY samples, all specimens with a girdle diameter

NGY STATIONS													
11*	12	13	14	15	16	41*	42	43	44	45	46		
Surface temperature	20,66	24,28	25,49	23,78	22,19	21,62	17,49	23,27	24,15	23,50	21,25	20,90	
Temperature at 100m	13,26	17,53	19,65	19,52	18,73	18,61	16,66	12,21	19,99	20,54	20,50	20,37	
(at 50m)	4	4	4	4	4	8	4	5	7	4	4	5	
Number slides examined	601	191	233	267	270	241	1803	318	92	197	184	241	365
Number ceratia counted													1397
<u>CERATIUM TRICHO CEROS</u>													
Random selection (Diam $\leq 42 \mu$)	3,99%	19,37%	12,88%	11,24%	4,44%	3,32%	7,26%	1,57%	22,83%	8,12%	13,04%	8,71%	11,78%
of measured (Diam = 45μ)	9	18	9	4	4	5	49	-	5	1	6	-	3
specimens	-	-	1	1	1	-	3	-	-	-	-	-	-
(Diam $\geq 48 \mu$)	5	6	14	13	6	2	40	3	-	-	10	-	14
													27
<u>CERATIUM MASSILIENSE</u>													
VAR. MASSILIENSE	2,50%	5,24%	3,86%	0,75%	0,37%	1,66%	2,27%	2,52%	2,17%	3,55%	1,09%	1,66%	1,64%
Random selection (A $\geq 90^\circ$)	2	-	2	-	-	-	4	1	-	2	-	-	3
of measured (70° $\leq$ A $< 90^\circ$)	8	6	4	-	1	1	20	5	1	3	1	3	2
specimens (50° $\leq$ A $< 70^\circ$)	3	1	-	1	-	-	5	-	-	-	-	-	-
<u>CERATIUM MASSILIENSE</u>													
VAR. CARRIENSE	-	2,09%	-	-	-	0,41%	0,28%	-	-	0,51%	2,72%	1,66%	-
Random selection (B $> 130^\circ$)	-	3	-	-	-	-	3	-	-	-	2	1	-
of specimens (B $< 130^\circ$)	-	1	-	-	-	1	2	-	-	1	3	3	-
													7
<u>CERATIUM DEFLEXUM F. DEFLEXUM</u>													
	-	1,57%	1,29%	1,87%	1,11%	0,41%	0,83%	0,69%	3,26%	0,51%	0,54%	0,41%	-
<u>CERATIUM DEFLEXUM F. DEFLECTOMASSUM</u>													
	-	-	-	-	-	0,37%	-	0,06%	-	-	0,51%	0,54%	0,55%
	-	-	5,58%	2,62%	1,48%	2,90%	1,72%	0,31%	1,09%	8,63%	5,98%	6,64%	3,84%
													4,22%
<u>CERATIUM MACROCEROS</u>													
	0,33%	7,85%	11,58%	6,36%	4,44%	4,14%	4,60%	6,28%	16,30%	7,61%	11,95%	12,03%	11,23%
													10,16%
<u>CERATIUM TENUE</u>													

TABLE 1.

Showing distribution and relative frequency, expressed as a percentage, of species of Subsection *Macroceras* in samples from the line of NGY stations off Port Elizabeth, which were examined in detail for the *Ceratium* flora. (Temperatures in °C. A = Left horn degree co-ordinate with 15 μ radius co-ordinate, B = Left horn degree co-ordinate.) For hydrographic data from the Agulhas current NGY stations, see Zoutendyk (1960).

No. NGY stns where ceratia recorded		Range of temps where ceratia recorded		Highest % abundance	
Feb-March	May	August	Highest s. temp	Lowest s. temp	in diatom-dinoflag.
(15 stns)	(29 stns)	(32 stns)	(+ temp at 100m)	(+ temp at 100m)	count per station
<u>C. VULTUR F. SUMATRANUM</u>					
(1)*	1	-	26,04	25,11	0,31%
			19,07	21,30	
<u>C. MACROCEROS</u>					
3(1)*	7	2	27,11	15,89	1,23%
			22,31	15,39(40m)	
<u>C. DEFLEXUM F. DEFLEXUM</u>					
1(1)*	1	-	27,11	24,17	0,32%
			22,31	20,88	
<u>C. DEFLEXUM F. DEFLECTOMASSUM</u>					
1	-	-	26,38	26,38	0,32%
			19,70	19,79	
<u>C. MASSILIENSE V. MASSILIENSE</u>					
2(1)*	5	-	27,11	18,03	0,61%
			22,31	15,49	
<u>C. MASSILIENSE V. CARRIENSE</u>					
1	2	-	25,49	24,17	0,31%
			19,65	20,88	
<u>C. TENUE</u>					
3	9	8	27,11	15,89	1,25%
			22,31	15,39(40m)	
<u>C. TRICHOEROS</u>					
3(2)*	13	5(1)*	27,11	15,96	1,23%
			22,31	10,45	

TABLE 2.

Showing frequency of species of Section *Macroceras* Ostf. in the general diatom-dinoflagellate counts for Agulhas current NGY stations. (76 N50V net samples were taken over three cruises during I.G.Y. 1958. The relative frequency of phytoplankton taxa was assessed by examining diluted drops of samples and enumerating the first 300-600 diatom cells, plus any dinoflagellates encountered. A total of 30 313 diatom cells and 874 armored dinoflagellates, of which 417 were ceratia, was counted.) * = stations where taxa were observed, but not during the count.

$\geq 45 \mu$ could be classified as *var. contrarium*, and those with a diameter $< 45 \mu$ as *var. trichoceros*, because of the nature of the base of the left horn and overall antapical horn curvature. In the literature, when the diameter can only be calculated from the figure, it is sometimes difficult to decide which variety is being described, particularly when the scale is doubtful, as in the cases of Cleve's figure of "*C. flagelliferum*" and Schiller's figure of *C. trichoceros*, by implication of *var. trichoceros*, (1937, Fig. 470), where the diameters are estimated as $\leq 42 \mu$, but antapical horn curvature and the nature of the base of the left horn, especially in Schiller's figure, are more typical of *var. contrarium*. Steemann Nielsen (1934) treated specimens from the Dana Pacific stations with diameters $< 42 \mu$ as *C. trichoceros* and $\geq 45 \mu$ as '*C. contrarium*'.

Apical horn length varies from about 150–600 μ ; in NGY specimens, there was little difference in horn length between the varieties; tips of antapical horns were generally below level of apex of apical horn, sometimes tips of all three horns were at same level; Entz (1902 Fig. 43) depicts a specimen of *C. trichoceros*, variety uncertain, in which the length of the antapical horns exceeds that of the long apical horn.

Distribution: *C. trichoceros* is a common species recorded from all oceans and the Mediterranean. Steemann Nielsen (1934, 1939) considered both *var. trichoceros* and *var. contrarium* to be surface species, but Graham & Bronikowsky (1944) found more records of *var. trichoceros* at 100 m than at upper levels in the Carnegie samples. Both authors found *var. contrarium* in tropical and subtropical waters, while *var. trichoceros* appeared to be a more strictly tropical taxon. *In situ* temperatures recorded by Graham & Bronikowsky for *var. trichoceros* were 14.0–29.4°C, and for *var. contrarium*, 10.2–29.5°C. Steemann Nielsen and Sournia (1967) found *var. trichoceros* to be indifferently oceanic and neritic, and *var. contrarium* clearly oceanic. This is supported by the records of Davis & Steidinger (1966) and Steidinger & Williams (1970) for neritic waters off Florida. In the numerical survey of Agulhas current NGY stations phytoplankton, a distinction between the two varieties was, unfortunately, not made. However, random measurements of girdle diameters show that for the neritic stations off Port Elizabeth, NGY 11 and 41, at least 5/24 and 3/5 specimens, respectively, could be classified as *var. contrarium*. (See Tables 1 and 2.)

Earlier records for the Agulhas current and S. W. Indian ocean are those of Karsten (1907) and Nel (1968), who used Karsten's nomenclature, recording *C. trichoceros*, '*C. tripos flagelliferum*', and its varieties '*angusta*', '*crassa*' and '*major*', Taylor (1967) and Thorrrington Smith (1969), both of whom did not distinguish between the varieties.

Ceratium trichoceros var. trichoceros

C. trichoceros (Ehrenberg) Kofoid (1908a): 362, Fig. 16–19; (1908b): 338;

Jørgensen (1911): 75, Pl. 9, Fig. 159a, b; (1920): 95, Fig. 85; Schröder (1911): 647 (as *C. trichoceros*); Forti (1922): 71, Pl. 5, Fig. 57 (= Jørgensen Fig. 159a); Pavillard (1931): 90, Pl. 3, Fig. 4; Böhm (1931a): 363; (1931b): 40; Wang & Nie (1932): 303, Fig. 15; Peters (1932): 51, Pl. 1, Fig. 3a-c, *non* Pl. 4, Fig. 17a (= *var. contrarium*); Steemann Nielsen (1934): 27, Fig. 68; (1939): 15; Nie (1936): 70, Fig. 32a, b and ? c (could be *var. contrarium*); Schiller (1937): 430, Fig. 470; Graham & Bronikowsky (1944): 40, Fig. 22B; Silva (1949): 361, Pl. 7, Fig. 4; Wood (1954): 311, Fig. 239a; Halim (1960): 180, Pl. 5, Fig. 18; (1963): 499, Fig. 31; Ballantine (1961): 225, Fig. 57; Klement (1964): 358; López (1966): 333, Figs. 44, 45; Davis & Steidinger (1966) Figs. 1-4; Sournia (1967): 472, Fig. 89; Steidinger & Williams (1970): 47, p.p., Fig. 36a-d, (includes *var. contrarium*).

C. flagelliferum Cleve (1900a): 14, e.p., Pl. 7, Fig. 12; (1900b): 217, e.p.; (both include *var. contrarium*); Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 6 *non* 7 (= *var. contrarium*).

C. tripos flagelliferum (Cleve) Karsten (1906): 145, 148, Pl. 22, Fig. 31b *non* 31a, c, d (= *var. contrarium*).

C. tripos flagelliferum f. crassa Karsten (1906): 146, 148, Pl. 22, Fig. 32a *non* b (= *var. contrarium*); *nec* Karsten (1907) Pl. 49, Fig. 25a-c (= *C. massiliense var. massiliense*).

C. tripos flagelliferum f. atlantica Stüwe (1909): 274, Pl. 1, Fig. 10 (if scale correct).

C. trichoceros f. crassum (Karst.) Jørgensen (1911): 76.

C. contrarium: Margalef (1957): 47, Fig. 3f; Paredes (1969/70): 42, e.p., Pl. 21, Fig. 147 (includes *var. contrarium*).

C. trichoceros var. contrarium: Klement (1964): 358, Pl. 3, Fig. 5.

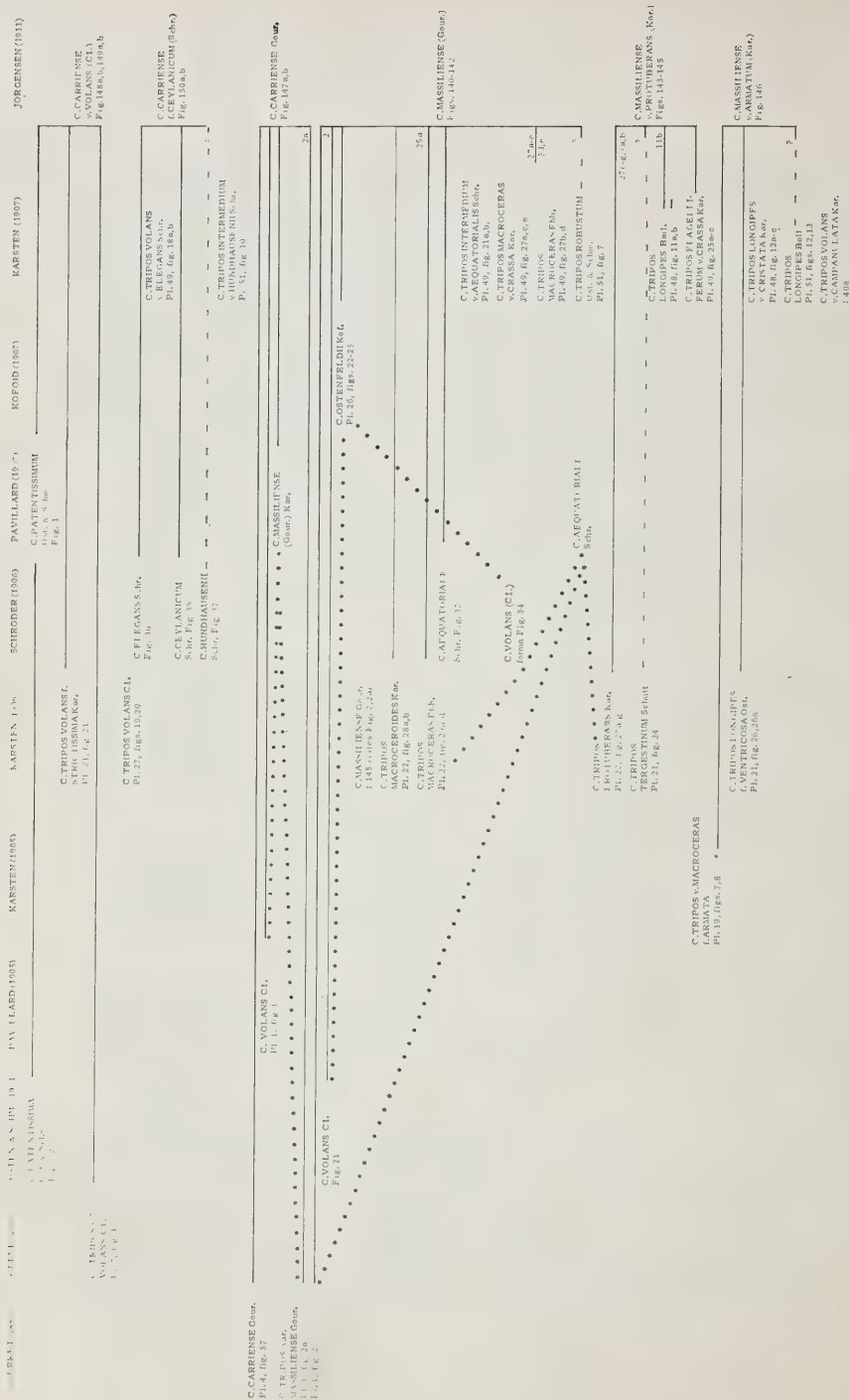
Peridinium trichoceros Ehrenberg (1860): 791; (1873): 3, Pl. 1, Fig. 1.

? *Non C. flagelliferum var. filiformis* Okamura & Nishikawa (1904): 123, Pl. 1, Fig. 11 (? = *C. tenue*).

Nomen nudum: *C. tripos var. flagellifera* Cleve (1899): 3.

Diagnosis: Differs from *var. contrarium* in having the girdle diameter $< 45 \mu$, or a diameter 45–48 μ and a “kink” at the base of the left horn and/or the ratio $\frac{RMBC}{D}$ exceeding 1.75.

Dimensions: In *NGY* specimens: Girdle diameter 30–42 μ , mostly 36–42 μ ; length left profile of hypotheca from base of horn to lower girdle list, 18–27 μ ; length epitheca, seen dorsally, from centre of upper girdle list to base of apical horn, 15–27 μ ; length apical horn 150–465 μ . From literature: diameter: 37–48 μ (Jørgensen 1911), 31–42 μ (Böhm 1931b), 40 μ (Wang & Nie 1932); 33–42 μ (Steemann Nielsen 1932), 41–45 μ (Silva 1949), 40 μ (Halim 1960), 44 μ (Halim 1963), 43 μ (Klement 1964), 38.4–45.5 μ (Davis & Steidinger 1966), as low as 31



μ (Steidinger & Williams 1970, who included specimens of *var. contrarium* with diameters $> 48 \mu$ in the range of measurements given); length apical horn 200–420 μ (Jørgensen 1911).

Böhm (l.c.), on examination of 208 specimens at 7 stations, found that diameter decreased with increase in temperature. This was confirmed by Steemann Nielsen (1934), who also found that the diameter tended to increase in size in neritic conditions; he found further, that antapical horns tended to be shorter in specimens from oceanic stations. These observations were not supported by random measurements of NGY Agulhas current specimens.

Ceratium trichoceros var. contrarium (Gourret) Schiller (1937): 431, Fig. 471 (= Jørgensen (1911) Fig. 160a).

Rampi (1939): 310, Fig. 39; Wood (1954): 311, Fig. 239b; Steidinger & Williams (1970): 47; non Klement (1964): 358, Pl. 3, Fig. 5 (= *var. trichoceros*).

C. tripos var. contrarium Gourret (1883): 32, Pl. 3, Fig. 51.

C. tripos contrarium: Karsten (1906): 145, 147, Pl. 22, Fig. 30a, b.

C. contrarium (Gourret) Pavillard (1905): 53, Pl. 2, Fig. 1; (1907): 229; (1931): 89, Pl. 3, Fig. 3; (1937): 9; Jørgensen (1920): 93, Fig. 84; Paulsen (1930): 90, Fig. 58A–C; Böhm (1931a): 363; (1931b): 40; Peters (1932): 50, Pl. 2, Fig. 10c; Steemann Nielsen (1934): 27, Fig. 67; (1939): 15; Graham & Bronikowsky (1944): 40, Fig. 24A non 22E (= *C. massiliense*); Silva (1949): 361, Pl. 9, Fig. 12; Halim (1960): 179; (1963): 499, Fig. 30; Margalef & Duran (1953): 42; Wood (1963): 7; López (1966): 333, Fig. 46; Sournia (1967): 472, Fig. 89; Paredes (1969/70): 42, e.p., non Pl. 21, Fig. 147 (= *var. trichoceros*); non Margalef (1957): 47 Fig. 3f (= *var. trichoceros*).

C. tripos var. macroceras f. contraria (Gourret) Schröder (1901): 16.

C. tripos var. inflexum Gourret (1883): 29, Pl. 3, Fig. 44.

C. inflexum (Gourret) Kofoid (1908b): 388; Jørgensen (1911): 76, Pl. 9, Figs. 160a, b, 161 a, b; Schröder (1911): 647; Pavillard (1916): 18; Forti (1922): 72, Pl. 5, Fig. 58 (= Jørgensen Fig. 161a); Abè (1927): 432, Fig. 50; non Schröder (1906): 362 (belongs to Section *Tripos*, as Schröder describes the “antapex” as “etwas gewolbt”).

? *C. tripos var. macroceras f. inflexa* (Gourret) Schröder (1900): 16, e.p., non Pl. 1, Fig. 17h (= *C. contortum var. karstenii* (Pav.) Sour. according to Jørgensen (1920: 75)).

C. flagelliferum Cleve (1900a): 14, e.p., non Pl. 7, Fig. 12 (= *var. trichoceros*); (1900b): 217, p.p., (includes *var. trichoceros*).

C. tripos flagelliferum (Cleve) Karsten (1906): 145, 148, Pl. 22, Fig. 31 a, c, d. non b (= *var. trichoceros*).

C. tripos flagelliferum f. crassa Karsten (1906): 146, 148 Pl. 22, Fig. 32b non a (= *var. trichoceros*); non (1907): 410, Pl. 49, Fig. 25a–c (= *C. massiliense*).

LEFT HORN DEGREE COORDINATE WITH THE 150 μ RADIUS COORDINATE

< 120°	120-124°	125-129°	130-134°	135-139°	≥ 140°
7GO 83 57 CC 63,70					
7GO 83 2A CTM 75		7GO 83 2A CTM 60			7GO 83 2 CTM 60,75
+CL 00 4 CV 64					
7OS 01 22 CP 67					
7OS 01 21 CV 75	7OS 01 21 CV 69				
7FA 07 1A CP 69			7FA 05 1 CV 69		
7FA 07 1B CP 70					
7FA 16 4 CCV 69					
7FA 23 C CCVP 63,69		+PA 31 6 CC 74			
*SH 06 35 CC 90					*SH 06 32 CA 100
*SH 06 36 CE 108					*SH 06 34 CV 88
*SH 06 37 CH 90					
*KA 06 19A CTV 104					
*KA 06 19B CTV 96					
*KA 06 21 CTVS 96					
*KA 07 18A CTV 72					
*KA 07 18B CTV 88					
*KA 07 27D CTM 88					
*KA 07 27E CTM 104					
*OK 07 2A CP <65, >65					
*OK 07 2B CP <65, >65					
+OK 07 2C CP 70					
+OK 07 18B CV 72				+OK 07 18C CV 64	+OK 07 18D CV 62
	+KO 07 25 CO 73				*OK 07 18E CV ≥ 60
+JO 11 148 CCV 63	+JO 11 147 CC 72	7JO 11 150 CC 60,66			+KO 07 22 CO 73
7JO 11 149 CCV 60,69					+KO 07 23 CO 66
+FO 22 54 CC 75					
+PU 30 57A CC 75					
+PU 30 57C CC 63					
7BO 31 18B CME 66	7BO 31 17B CME 66	7BO 31 18A CME 75			7BO 31 17A CME 60,69
+SH 34 64 CCV 64					
+SL 37 464B CC 60					
+GB 44 22A CC 75					
7MD 53 12L CCV 70			7MD 53 12N CM 73	7MD 53 12M CM 66	7MD 53 12K CH 73
+HA 60 11 CCV 72					
+HA 63 28 CHM 66					
+LO 66 47 CC 63					
+LO 66 48 CC 63	+LO 66 48 CC 65				
+LO 66 49 CCV 70	+LO 66 50 CM 70				
+LO 66 51 CM 80					
7SW 70 13A CC 66					
7SW 70 14A CCV 72					
-NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY					
NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY		NGYNGYNGYNGYNGY	+ 49 SPECIMENS
NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY		NGYNGYNGYNGYNGY	NGYNGYNGYNGYNGY
NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY	-NGYNGYNGYNGYNGY			

LEFT HORN DEGREE COORDINATE WITH 300 μ RADIUS COORDINATE

$\leq 120^\circ$	120-129 $^\circ$	130-139 $^\circ$	$\geq 140^\circ$	$\geq 140^\circ$
?GO 83 57 CC 63,70 +CL 00 4 CV 64 ?OS 01 22 CP 67 ?PA 07 1A CP 69 ?PA 07 1B CP 70 ?PA 23 C CCVP 63,69 *SH 06 35 CC 90 *SH 06 36 CE 108 *KA 06 19A CTV 104 *KA 06 21 CTVS 96 *KA 07 18A CTVE 72 *KA 07 18B CTV 88 *OK 07 2C CP 70 *OK 07 2B CP > 65 *OK 07 18B CV 72 +JO 11 148 CCV 63 ?JO 11 149 CCV 60,69 +FU 30 57A CC 75 +GB 44 22A CC 75	?GO 83 57 CC 63,70 +CL 00 4 CV 64 ?PA 16 4 CCV 69 *SH 06 37 CH 90 *KA 06 19B CTV 96 *KA 07 27D CTH 88 *OK 07 2A CP > 65 *OK 07 2B CP < 65 ?BO 31 18B CME 66 +SN 34 64 CCV 64 +LO 66 49 CCV 70	?GO 83 57 CC 70 +CL 00 4 CV 64 ?OS 01 21 CV 69,75 +PA 31 6 CC 74 *KA 07 27E CTHG 104 *OK 07 2A CP < 65 +JO 11 147 CC 72 ?JO 11 150 CCV 60,66 +FO 22 54 CC 75 ?MD 53 12L CCV 70 +LO 66 47 CC 63 +LO 66 51 CH 80 ?SW 70 13A CC 66	?GO 83 2A CTH 60,75 +XO 07 25 CC 73 +FU 30 57C CC 63 ?BO 31 18A CME 75 ?BO 31 17B CME 66 +SL 37 464B CC 60 +HA 60 11 CCV 72 +HA 63 28 CHM 66 +LO 66 48 CC 65 +LO 66 50 CH 70	?GO 83 2 CTH 60,75 ?PA 05 1 CV 69 *SH 06 34 CV 88 *SH 06 32 CA 100 +OK 07 18C CV 64 +OK 07 18D CV 62 *OK 07 18E CV $\geq$ 60 +XO 07 22 CC 73 +XO 07 23 CC 66 ?BO 31 17A CME 60,69 ?MD 53 12K CH 73 ?MD 53 12M CH 66 ?MD 53 12N CH 73 + 49 SPECIMENS NGYNGYNGYNGYNGY

LEFT HORN DEGREE COORDINATE WITH 150 μ RADIUS COORDINATE $< 130^\circ$ (VAR. *CARRIENSE*)LH $^\circ$ AT 150 μ RC $\geq 130^\circ$ (VAR. *MASSILIENSE*)

TABLE 4.

Showing variation in left horn degree co-ordinates with the 150 μ radius co-ordinates in *C. massiliense* (Gour.) Karst., in specimens from the Agulhas current NGY samples and in a selection of figures from the literature. The latter are referred to in sequence by author, year of publication, figure number, name used and diameter in μ which determined scale of photographic enlargement; in specimens underlined, co-ordinates are estimated. (BO Böhm, CL Cleve, FO Forti, GB Graham & Bronikowsky, GO Gourret, HA Halim, JO Jörgensen, KA Karsten, KO Kofoid, LO López, MD Margalef & Duran, OK Okamura, OS Ostenfeld & Schmidt, PA Pavillard, PU Paulsen, SH Schröder, SL Schiller, SN Steemann Nielsen, SW Steidinger & Williams; ? = original scale of figure not known, * = scale of figure known, but possibly incorrect, + = scale of figure known and probable, — = NGY specimens in which left horn degree co-ordinate with 300 μ radius co-ordinate is $> 130^\circ$.)

[illegible]

TABLE 5.

C. trichoceros (Ehb.) Kof.: Showing variation in the ratio $\frac{\text{RMBc}}{\text{D}}$ (right horn MBC radius co-ordinate in radius units/girdle diameter in radius units) in relation to the girdle diameter in specimens from NGGY Agulhas current stations and from the literature. (AB, Abè (1927); BA, Ballantine (1961); CLEV, Cleve (1900ad); D & S, Davis & Steidinger (1967); EHRB, Ehrenberg (1873); GE, Graham & Bronikowsky (1944); GO, Gourret (1883); HA, Halim (1960, 1963); J, Jørgensen (1911); K, Karsten (1906, 1907); KLE, Kleven (1964); KOR, Koroid (1908a); LO, Lopez (1966); MA, Margalef (1957); N, Nie (1936); O&N, Okamura & Nishikawa (1904); PAV, Pavillard (1931); PR, Paredes (1969/70); PU, Paulsen (1930); RA, Rampi (1939); SN, Steenmann Nielsen (1934); SW, Steidinger & Williams (1970); SD, Schröder (1900); SH, Schiller (1937); SIL, Silva (1949); SO, Sourina (1967); STUW, Stuwé (1909); WN, Wang & Nie (1932); indicators $\frac{\text{D}}{\text{RMBc}} \geq 1.75$ and basal kink in the left horn absent in left horn; XXXXXX refers to NGGY specimens, were all with a girdle diameter ≥ 45 mm; RMBc = basal kink in the left horn).

C. tripos flagelliferum f. angusta Karsten (1906): 146, 148, Pl. 22, Fig. 33a *non b* (= *C. tenue*).

C. tripos flagelliferum var. angusta Karsten (1907): 410, 411, Pl. 49, Fig. 24a, *non b, c* (*b* = *C. massiliense* (on account of size), *c* = *C. tenue*).

C. tripos flagelliferum var. major Karsten (1907): 410, Pl. 49, Fig. 22a–d.

C. tripos var. macroceras f. claviceps Schröder (1900): 16, Pl. 1, Fig. 17 n, (as Jörgensen (1920: 75) indicates, scales given by Schröder are incorrect).

C. inflexum f. claviceps (Schröder) Jörgensen (1911): 76; Schröder (1911): 647, Fig. 12.

C. trichoceros f. claviceps (Schröder) Schiller (1937): 431; Rampi (1939): 311; Wood (1954): 312, ? Fig 239c (in this figure, tips of antapical horns not shown), *non* Fig. 239d (unnamed figure with clavate horn tips, from curvature of horns = *C. tenue*).

C. contrarium f. claviceps (Schröder) Jörgensen (1920): 94.

C. contrarium var. claviceps (Schröder) Graham & Bronikowsky (1944): 40, Fig. 24B; Halim (1960) Pl. 5, Fig. 14.

C. trichoceros var. contrarium f. claviceps: Davis & Steidinger (1966).

C. tripos flagelliferum var. undulata Karsten (1907): 410, Pl. 49, Fig. 23.

Non C. tripos macroceras f. undulata Schröder (1900): 16, Pl. 1, Fig. 17kum (*k* = *C. massiliense*, *l* = *c. tenue* (also according to Pavillard (1931) but not Jörgensen (1911, 1920) who considered it to be *var. contrarium*), *m* = *C. vultur var. pavillardii* (Jörg.) Rein. (considered by Jörgensen (1920: 87, 92 to be both *C. massiliense* and *var. pavillardii*).

C. tripos var. typicum Gourret (1883): 31, Pl. 2, Fig. 36; Daday (1888): 99.

C. tripos var. Gouretii Lemmermann (1901): 636.

C. trichoceros: Peters (1932): 51, e.p., Pl. 4, Fig. 17a (includes *var. trichoceros*); Abè (1927): 431, Fig. 49; Rampi (1939): 310, Fig. 39.

C. horridum subsp. tenue: Dangeard (1927): 379, Fig. 43a, *non C. tenue* O. & S.

C. massiliense: Paulsen (1930) Fig. 55A, B *non C–F* (= *C. massiliense*), *non*

C. massiliense (Gourret) Karsten.

“Typenkreise der Gattung *Ceratium*”: Schütt (1892): 267, Fig. 77Vb.

Diagnosis: Differs from *var. trichoceros* in that the girdle diameter is $> 48 \mu$, or $45\text{--}48 \mu$ with the ratio $\frac{RMBC}{D} < 1.75$ and no “kink” at base of left horn.

Dimensions: In *NGY* specimens: Girdle diameter $45\text{--}60 \mu$, mostly $48\text{--}54 \mu$; length hypotheca $24\text{--}39 \mu$; length epitheca $21\text{--}36 \mu$; length apical horn $160\text{--}620 \mu$. From literature: diameter: $51\text{--}68 \mu$ (Jörgensen 1911), $59\text{--}64 \mu$ (Paulsen 1930), $45\text{--}60 \mu$ (Stemann Nielsen 1934), 48μ (Paredes 1969/70), up to 61μ (Steidinger & Williams 1970, who included specimens of *var. trichoceros*, with diameters $< 45 \mu$ in the range of measurements given); apical horn $300\text{--}560 \mu$ (Jörgensen 1911).

Steemann Nielsen (1934) found that diameter showed an increase in size with a decrease in temperature. Random measurements of NGY specimens were insufficient to substantiate this.

The distal parts of the apical and antapical horns generally lie parallel to one another: six specimens were found in the NGY samples where the antapical horns diverged to a varying degree from one another and the apical horn. These were similar to cells referred to by Karsten (1907) as *C. tripos flagelliferum* var. *major*. In the graphs of antapical horn curvature they are shown separately as var. *contrarium* B, but they do not differ sufficiently to be treated as a distinct taxon, (See Figs. 13A–C, 24E).

The separation of specimens with clavate antapical horn tips as a distinct taxon is not justified, as a range of variation, from antapical horns with rounded, to slightly clavate, to very expanded tips, is found. Graham & Bronikowsky (1944) found specimens with clavate tips rather frequent in the N. Atlantic and Pacific; they were not recorded by Sournia (1967) and only two were seen in the present survey.

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